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Connectivity of Streams and Wetlands to Downstream Waters: A Review and Synthesis of the Scientific Evidence

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3.3. INFLUENCE OF STREAMS AND WETLANDS ON DOWNSTREAM WATERS

The previous section provided background on river system hydrology. In this section, we provide a general overview of how streams and wetlands affect downstream waters, focusing on functions within streams and wetlands and their connectivity to rivers.

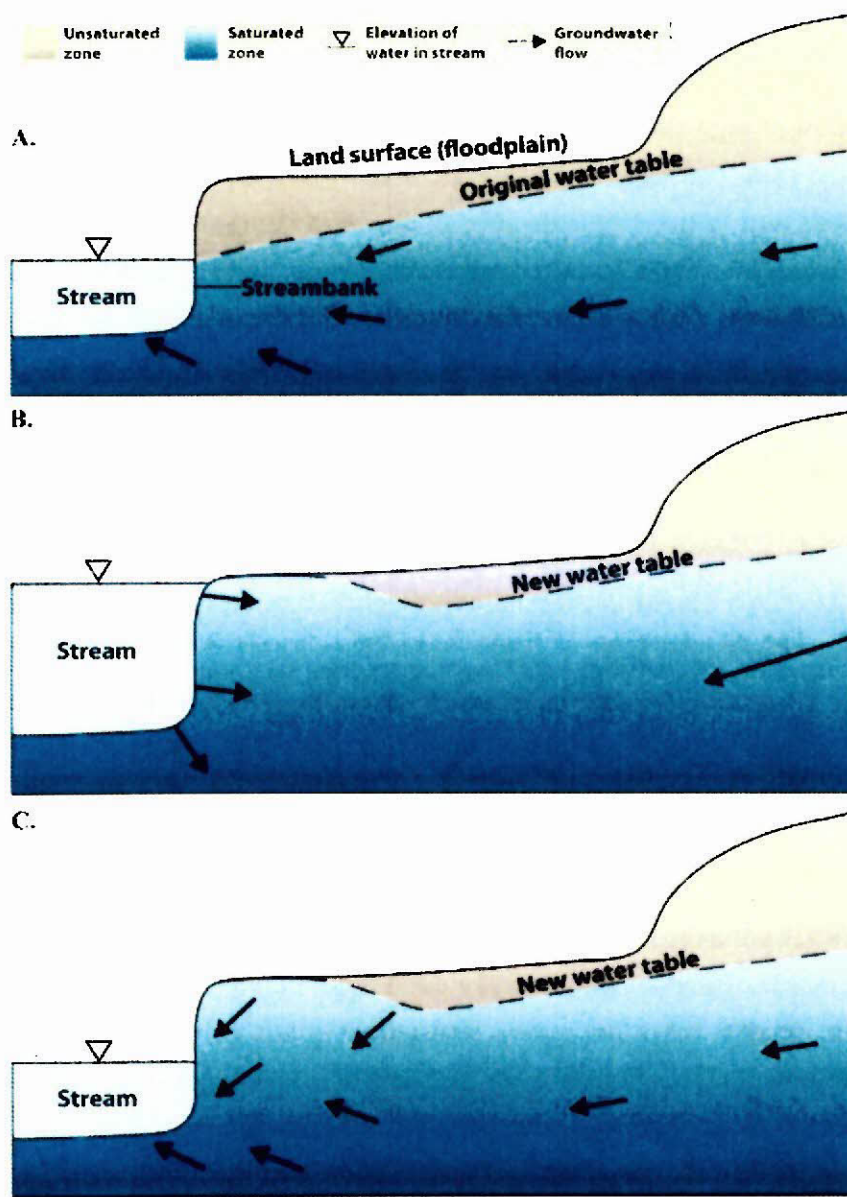


Figure 3-13. The direction and magnitude of surface water-groundwater interactions can dramatically change during large hydrological events, including floods. (A) In a hypothetical stream-floodplain cross-section, groundwater flows from the alluvial aquifer to the stream prior to a major hydrological event. (B) During the bank-full hydrologic event, surface water moves from the stream and becomes groundwater in the alluvial aquifer. (C) After recession of the event water in the stream channel, groundwater that was stored in the alluvial aquifer during the hydrologic event flows back to the stream. This process is called bank storage and can sustain baseflow in streams and rivers after the hydrologic event has ended.

Modified from Winter et al. (1998).

1 The structure and function of rivers are highly dependent on the constituent materials that
2 are stored in and transported through them. Most of these materials, broadly defined here as any
3 physical, chemical, or biological entity, including water, heat energy, sediment, wood, organic
4 matter, nutrients, chemical contaminants, and organisms, originate outside of the river: they
5 originate from either the upstream river network or other components of the river system, and
6 then are transported to the river by water movement or other mechanisms. Thus, the
7 fundamental way in which streams and wetlands affect river structure and function is by altering
8 fluxes of materials to the river. This alteration of material fluxes depends on two key factors:
9 functions within streams and wetlands that affect material fluxes, and connectivity (or isolation)
10 between streams and wetlands and rivers that allows (or prevents) transport of materials between
11 the systems.

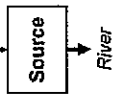
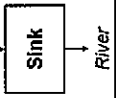
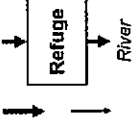
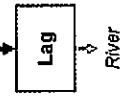
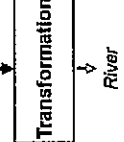
12 13 **3.3.1. Effects of Streams and Wetlands on Material Fluxes**

14 Streams and wetlands affect the amounts and types of materials that are or are not
15 delivered to downstream waters, ultimately contributing to the structure and function of those
16 waters. Leibowitz et al. (2008) identified three functions, or general mechanisms of action, by
17 which streams and wetlands influence material fluxes into downstream waters: **source**, **sink**, and
18 **refuge**. We have expanded on this framework to include two additional functions: **lag** and
19 **transformation**. These five functions (summarized in Table 3-1) provide a framework for
20 understanding how physical, chemical, and biological connections between streams and wetlands
21 and downstream waters influence river systems.

22 These five functions (see Table 3-1) are neither static nor mutually exclusive, and often
23 the distinctions between them are not sharp. A stream or wetland can provide different functions
24 at the same time, and these functions can vary with the material considered (e.g., acting as a
25 source of organic matter and a sink for nitrogen) and can change over time (e.g., acting as a
26 water sink when evapotranspiration is high and a water source when evapotranspiration is low).
27 The magnitude of a given function also is likely to vary temporally: For example, streams
28 generally are greater sources of organic matter and contaminants during high flows.

29 Leibowitz et al. (2008) explicitly focused on functions that benefit downstream waters,
30 but these functions can also have negative effects—for example, when streams and wetlands
31 serve as sources of chemical contamination (see Table 3-1 and Sections 4.4.3, 5.3.2.6, 5.3.2.5,
32 and 5.4.3.1). In fact, benefits need not be linear with respect to concentration; a beneficial
33 material could be harmful at higher concentrations due to nonlinear and threshold effects. For
34 example, nitrogen can be beneficial at lower concentrations but can reduce water quality at

Table 3-1. Functions by which streams and wetlands affect material fluxes to downstream waters

Function	Definition	Examples
	Net increase in a material flux (exports > imports)	<i>Streams</i> : invertebrate production (Wipfli and Gregovich, 2002) <i>Wetlands</i> : phytoplankton production from floodplain (Schemel et al., 2004; Lehman et al., 2008)
	Net decrease in a material flux (exports < imports)	<i>Streams</i> : upstream fish populations that are not sustainable without net immigration from downstream areas (Woodford and McIntosh, 2010) <i>Wetlands</i> : sediment deposition, denitrification (Johnston, 1991)
	Avoidance of a nearby sink function, thereby preventing a net decrease in material flux (exports = imports)	<i>Streams</i> : headwaters as summer coldwater refuges (Curry et al., 1997) <i>Wetlands</i> : riparian wetlands as aquatic refuges in dryland rivers (Leigh et al., 2010)
	Temporary storage and subsequent release of materials without affecting cumulative flux (exports = imports); delivery is delayed and can be stretched out	<i>Streams</i> : delay of downstream peak flows due to bank storage (Burt, 1997); temporary heat storage within the alluvial aquifer (Arrigoni et al., 2008) <i>Wetlands</i> : flood attenuation (Bullock and Acreman, 2003)
	Conversion of a material into a different form; the amount of the base material is unchanged (base exports = base imports), but its composition (i.e., mass of the different forms) can vary	<i>Streams</i> : conversion of coarse to fine particulate organic matter (Wallace et al., 1995) <i>Wetlands</i> : mercury methylation (Galloway and Branfireun, 2004; Selvendiran et al., 2008)

Notes: Arrows indicate material imports to and exports from a stream or wetland, in terms of mass; arrow widths represent relative material mass and differences in arrow shades represent timing (lag) or composition (transformation) changes. Imports into streams and wetlands can come from upland terrestrial areas, other streams and wetlands, or from the river itself. Arrows are meant to be illustrative, and do not necessarily represent upstream/downstream relationships. For example, materials can move downstream, upstream, or laterally into streams and wetlands. Examples of commonly exchanged materials include water, heat energy, nutrients, contaminants, sediment, particulate organic matter, organisms, and reproductive propagules; note that exchange of materials between streams and wetlands and downstream systems can result in positive or negative effects on downstream waters.

1 higher concentrations. Although here we focus primarily on the effects of streams and wetlands
2 on downstream waters, these same functions can describe effects of downstream waters on
3 streams and wetlands (e.g., downstream rivers as sources of colonists for upstream tributaries).

4 Because many of these functions depend on import of materials into streams and
5 wetlands, distinguishing between *actual function* and *potential function* is instructive. For
6 example, a wetland with appropriate conditions (e.g., a reducing environment and denitrifying
7 bacteria) is a potential sink for nitrogen (see Sections 5.3.2.2 and 5.4.3.2): if nitrogen is imported
8 into the wetland, the wetland has the capacity to remove it by denitrification. The wetland will
9 not serve this function, however, if nitrogen is not imported. Thus, even if a stream and wetland
10 is not currently serving a function, it has the potential to provide the function under appropriate
11 conditions (e.g., when material imports or environmental conditions change). Although potential
12 functions do not actively affect downstream waters, they can play a critical role in protecting
13 those waters from future impacts. Ignoring potential function can also lead to the paradox that
14 degraded streams and wetlands (e.g., those receiving nonpoint-source nitrogen inputs) receive
15 more protection than less impacted systems (Leibowitz et al., 2008).

16 The effect that material fluxes from streams and wetlands have on downstream waters is
17 influenced by three factors: (1) proportion of the material originating from (or reduced by)
18 streams and wetlands relative to the importance of other system components, such as the river
19 itself; (2) residence time of the material in the downstream water; and (3) relative importance of
20 the material. In many cases, the effects on downstream waters need to be considered in
21 aggregate. For example, the contribution of material by a particular stream and wetland (e.g., a
22 specific ephemeral stream) might be small, but the aggregate contribution by an entire class of
23 streams and wetlands (e.g., all ephemeral streams in the river network) might be substantial.
24 Integrating contributions over time also might be necessary, taking into account duration and
25 frequency of material export and delivery. Considering the cumulative material fluxes, rather
26 than the individual materials separately, that originate from a specific stream and wetland is also
27 important in understanding the effects of material fluxes on downstream waters.

28 In general, the more frequently a material is delivered to the river, the greater its effect.
29 The effect of an infrequently supplied material, however, can be large if the material has a long
30 residence time in the river (Leibowitz et al., 2008). For example, woody debris might be
31 exported to downstream waters infrequently, but it can persist in downstream channels. Also,
32 some materials are more important than others in defining the structure and function of a river.
33 For example, woody debris can have a large effect on river structure and function because it
34 affects water flow, sediment and organic matter transport, and habitat (Harmon et al., 1986;
35 Gurnell et al., 1995), or salmon migrating to a river can serve as a keystone species that regulates
36 other populations and serves as a source of marine-derived nutrients (Schindler et al., 2005).

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3.3.2. Connectivity and Transport of Materials to and from Streams and Wetlands

3.3.2.1. *Connectivity and Isolation*

The functions discussed above represent general mechanisms by which streams and wetlands influence downstream waters. For these altered material fluxes to affect a river, however, transport mechanisms that deliver (or could deliver) these materials to the river are necessary. **Connectivity** describes the degree to which components of a system are connected and interact through various transport mechanisms; connectivity is determined by the characteristics of both the physical landscape and the biota of the specific system. This definition is related to, but is distinct from, definitions of connectivity based on the actual flow of materials between system components (e.g., Pringle, 2001). The concept that connectivity among river system components, including streams and wetlands, plays a significant role in the structure and function of these systems is not new. In fact, much of the theory developed to explain how these systems work has focused on connectivity and linkages between system components (e.g., Vannote et al., 1980; Newbold et al., 1982a; Newbold et al., 1982b; Junk et al., 1989; Ward, 1989; Benda et al., 2004; Thorp et al., 2006).

In addition to its central role in defining river systems (see Section 3.2.1), water movement through the river system (see Figure 3-6) is the primary mechanism providing physical connectivity both within river networks and between those networks and the surrounding landscape (Fullerton et al., 2010). Hydrologic connectivity results from the flow of water, which provides a “hydraulic highway” (Fausch et al., 2002) along which physical, chemical, and biological materials associated with the water are transported (e.g., sediment, woody debris, contaminants, organisms).

Ecosystem function within a river system is driven by interactions between its physical environment and the diverse biological communities living within it (Wiens, 2002; Schroder, 2006). Thus, river system structure and function also depend on biological connectivity among the system’s populations of aquatic and semiaquatic organisms. Biological connectivity refers to the movement of biota, either in terms of entire organisms or reproductive materials (e.g., seeds, eggs, genes), through river systems. These movements link aquatic habitats and populations in different locations through several processes important for the survival of individuals, populations, and species (see Sections 4.5, 5.3.3, and 5.4.4). Movements include dispersal, or movement away from an existing population or parent organism; migration, or long-distance movements undertaken on a seasonal basis; localized movement over an organism’s home range to find food, mates, or refuge from predators or adverse conditions; and movement to different habitats to complete life-cycle requirements. At the population and species levels, dispersal and migration contribute to persistence at local and regional scales via colonization of new habitats

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(e.g., Hecnar and McLoskey, 1996; Tronstad et al., 2007), location of mates and breeding habitats (Semlitsch, 2008), rescue of small populations threatened with local extinction (Brown and Kodric-Brown, 1977), and maintenance of genetic diversity (e.g., Waples, 2010). These movements can result from passive transport by water, wind, or other organisms (e.g., birds, terrestrial mammals), from active movement with or against water flow (e.g., upstream fish migration), or from active movement over land (for biota capable of terrestrial dispersal) or through the air (for birds or insects capable of flight). Thus, biological connectivity can occur within aquatic ecosystems or across ecosystem or watershed boundaries, and it can be multidirectional. For example, biota can move downstream from perennial, intermittent, and ephemeral headwaters to rivers, upstream from estuaries to rivers to headwaters, or laterally between floodplain wetlands, geographically isolated wetlands, rivers, lakes, or other water bodies. Significant biological connectivity can also exist between aquatic and terrestrial habitats (Nakano et al., 1999; Gibbons, 2003; Baxter et al., 2004), but here we focus on connections among components of aquatic systems.

As noted in Section 3.2.3, streams and rivers are not pipes (Bencala, 1993; Bencala et al., 2011); they provide opportunities for water to interact with internal components (e.g., alluvium, organisms) through the five functions by which streams and wetlands alter material fluxes (see Table 3-1). Connectivity between streams and wetlands provides opportunities for material fluxes to be sequentially altered by multiple streams and wetlands as the materials are transported downstream. The proportion of a material that ultimately reaches the river is determined by the aggregate effect of these sequential fluxes. The form of the exported material can change as it moves down the river network (see Figure 3-14), however, making quantitative assessments of the importance of individual stream and wetland resources within the entire river system difficult. For example, organic matter can be exported from headwater streams and consumed by downstream macroinvertebrates (see Figure 3-14). Those invertebrates can drift farther downstream and be eaten by juvenile fish that eventually move into the mainstem of the river, where they feed further and grow.

The assessment of stream and wetland influence on rivers is also complicated by the cumulative time lag resulting from these sequential transformations and transportations. For example, cations in stream water convert dissolved organic matter to fine particulate organic matter (FPOM, particle size <1 mm) that is taken up directly by benthic bacteria, delaying its export downstream.

The opposite of connectivity is **isolation**, or the degree to which transport mechanisms (i.e., pathways between system components) are lacking; isolation acts to reduce material fluxes between system components. Although here we primarily focus on the benefits that connectivity can have on downstream systems, isolation also can have important positive effects on the

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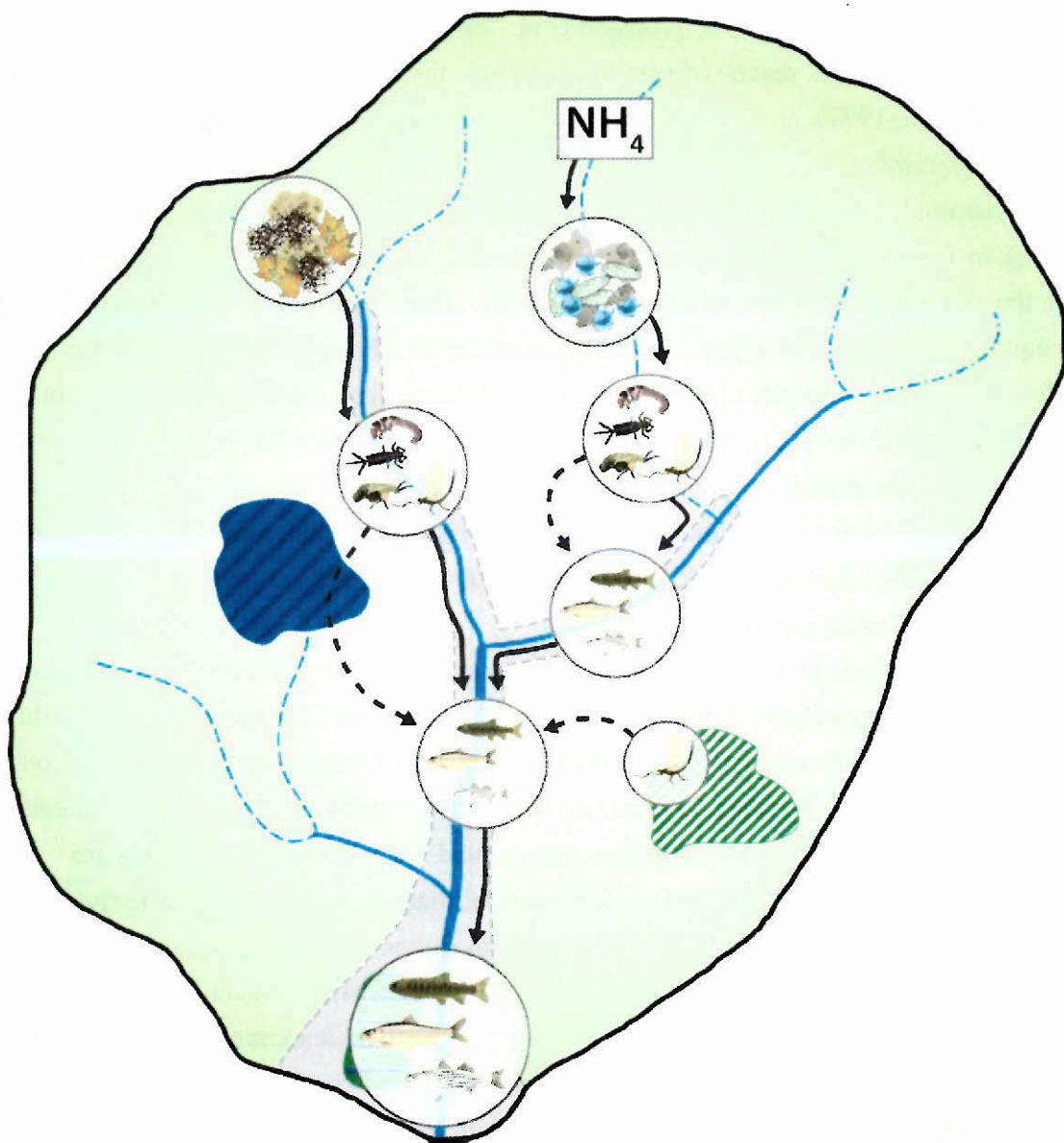


Figure 3-14. Illustration of the sequential transformation of materials as they move through the river network, via either downstream transport with water flow (solid black arrows) or via aerial or terrestrial movements (dashed black arrows). Here, an ephemeral headwater stream exports organic matter (at left) and an intermittent headwater stream exports ammonium, which is taken up and incorporated into algal biomass (at right). These basal food resources are eaten and transformed into macroinvertebrate biomass, which in turn is eaten and transformed into fish biomass in both local and downstream reaches.

condition and function of downstream waters. For example, waterborne contaminants that enter a wetland cannot be transported to a river if the wetland is hydrologically isolated from the river, except by terrestrial (overland) pathways. Increased isolation can decrease the spread of pathogens (Hess, 1996) and invasive species (e.g., Bodamer and Bossenbroek, 2008), and increase the rate of local adaptation (e.g., Fraser et al., 2011). Thus, both connectivity and isolation should be considered when examining material fluxes from streams and wetlands, and biological interactions should be viewed in light of the natural balance between these two factors.

When assessing the effects of connectivity/isolation and the five general functions (sources, sinks, refuges, lags, and transformation; see Table 3-1) on downstream waters, dimensions of time and space must be considered. Water or organisms transported from distant headwater streams or wetlands will generally require longer times for travel to a larger river than materials transported from streams or wetlands near the river (see Section 3.4.2). This can introduce a lag between the time when the function occurs and the time when the material arrives at the river. In addition, the distribution of streams and wetlands can be a function of their distance from the mainstem channel. For example, in a classic dendritic network there is an inverse geometric relationship between number of streams and stream order. In such a case, the aggregate level of function could potentially be greater for terminal source streams, compared to higher order or lateral source streams. This is one reason why terminal source stream watersheds often provide the greatest proportion of water for major rivers. However, connectivity results from many interacting factors (see Section 3.4.5). For example, the relationship between stream number and order can vary with basin shape and network configuration (see Section 3.4.2). Thus, caution must be exercised when making generalizations about these spatial and temporal relationships. Spatial and temporal variability of connectivity is discussed below, and the factors influencing them are considered in Section 3.4.

3.3.2.2. *Spatial and Temporal Variability of Connectivity*

Connectivity is not a fixed characteristic of a system, but rather varies over space and time (Leibowitz, 2003; Leibowitz and Vining, 2003). Variability in hydrologic connectivity results primarily from the longitudinal (see Figures 3-8 and 3-10) and lateral (see Figure 3-12) expansion and contraction of the river network and transient connection with other components of the river system (see Section 3.2.3).

The expansion and contraction of river networks affects the extent, magnitude, timing, and type of hydrologic connectivity. For example, intermittent and ephemeral streams (see Figure 3-7) only flow during wetter seasons (see Section 3.4) or during and immediately following precipitation events. Thus, the spatial extent of connectivity between streams and

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1 wetlands and rivers increases greatly during these high flow events because intermittent and
2 ephemeral streams are estimated to account for 59% of the total length of streams in the
3 contiguous United States (Nadeau and Rains, 2007b). Changes in the spatial extent of
4 connectivity due to expansion and contraction are even more pronounced in the arid and semiarid
5 Southwest, where more than 80% of all streams are intermittent or ephemeral (see Figure 3-9B;
6 Levick et al., 2008). Expansion and contraction also affect the magnitude of connectivity
7 because larger flows provide greater potential for material transport (e.g., see Section 4.3.2).

8 Besides affecting the spatial extent and magnitude of hydrologic connectivity, expansion,
9 and contraction of the stream network also affect the duration and timing of flow in different
10 portions of the network. Perennial streams have year-round connectivity with a downstream
11 river, while intermittent streams have seasonal connectivity. The temporal characteristics of
12 connectivity for ephemeral streams depend on the duration and timing of storm events.
13 Similarly, connectivity between wetlands and downstream waters can range from permanent to
14 seasonal to episodic.

15 The expansion and contraction of river systems also affect the type of connectivity. For
16 example, during wet periods when input from precipitation can exceed evapotranspiration and
17 available storage, unidirectional wetlands could have connectivity with other wetlands or streams
18 through surface spillage (Leibowitz and Vining, 2003; Rains et al., 2008). With cessation of
19 spillage due to drier conditions, hydrologic connectivity could only occur through groundwater
20 (Rains et al., 2006; Rains et al., 2008).

21 When dispersal, migration, and other forms of biotic movement are mediated by the flow
22 of water, biological and hydrologic connectivity can be tightly coupled. For example, seasonal
23 flooding of riparian/floodplain wetlands creates temporary habitat that fish, aquatic insects, and
24 other organisms use (Smock, 1994; Robinson et al., 2002; Tronstad et al., 2007). Factors other
25 than hydrologic dynamics can also affect the temporal and spatial dynamics of biological
26 connectivity. Such factors include movement associated with seasonal habitat use (Moll, 1990;
27 Lamoureux and Madison, 1999) and shifts in habitat use due to life history changes (Huryn and
28 Gibbs, 1999; Gibbons et al., 2006; Subalusky et al., 2009a), quality or quantity of food resources
29 (Smock, 1994), presence or absence of favorable dispersal conditions (Schalk and Luhring,
30 2010), physical differences in aquatic habitat structure (Grant et al., 2007), or the number and
31 size of nearby populations (Gamble et al., 2007). For a specific river system with a given spatial
32 configuration, variability in biological connectivity also occurs due to variation in the dispersal
33 distance of organisms and reproductive propagules (see Section 3.4.4; Semlitsch and Bodie,
34 2003).

35 Finally, just as connectivity from temporary or seasonal wetting of channels can have
36 effects on downstream waters, temporary or seasonal drying can also affect river networks.

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Riverbeds or streambeds that temporarily go dry are utilized by aquatic biota having special adaptations to wet and dry conditions, and can serve as egg and seed banks for a number of organisms, including aquatic invertebrates and plants (Steward et al., 2012). These temporary dry areas can also affect nutrient dynamics due to reduced microbial activity, increased oxygen availability, and inputs of terrestrial sources of organic matter and nutrients (Steward et al., 2012).

3.4. FACTORS INFLUENCING CONNECTIVITY

Numerous factors affect physical, chemical, and biological connectivity within river systems. These factors operate at multiple spatial and temporal scales, and interact with each other in complex ways to determine where components of a system fall on the connectivity-isolation gradient at a given time. In this section, we focus on five key factors: climate, watershed characteristics, spatial distribution patterns, biota, and human activities and alterations. These are by no means the only factors influencing connectivity, but they illustrate how physical, chemical, and biological connectivity are shaped by many different variables. We also examine how interactions among different factors influence connectivity, using wetlands in the prairie pothole region as a case study.

3.4.1. Climate-Watershed Characteristics

The movement and storage of water in watersheds varies with climatic, geologic, topographic, and edaphic characteristics of river systems (Winter, 2001; Wigington et al., 2012). At the largest spatial scale, climate determines the amount, timing, and duration of water available to watersheds and river basins. Key characteristics of water availability that influence connectivity include annual water surplus (precipitation minus evapotranspiration), timing (seasonality) of water surplus during the year, and rainfall intensity.

Annual runoff generally reflects water surplus and varies widely across the United States (see Figure 3-15). Seasonality of water surplus during the year determines when and for how long runoff and groundwater recharge occur. Precipitation and water surplus in the eastern United States is less seasonal than in the West (Finkelstein and Truppi, 1991). The Southwest experiences summer monsoonal rains (see Section 4.8), while the West Coast and Pacific Northwest receive most precipitation during the winter season (Wigington et al., 2012). Throughout the West, winter precipitation in the mountains occurs as snowfall, where it accumulates in seasonal snowpack and is released during the spring and summer-melt seasons to sustain streamflow during late spring and summer months (Brooks et al., 2012). The flowing portions of river networks tend to have their maximum extent during seasons with the highest

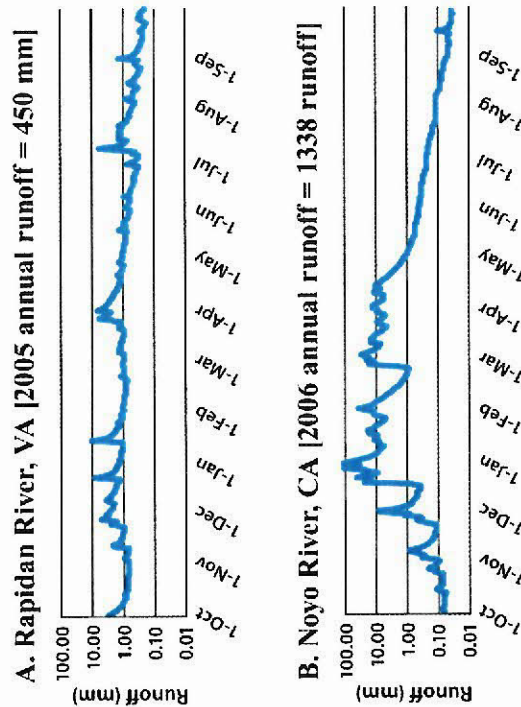
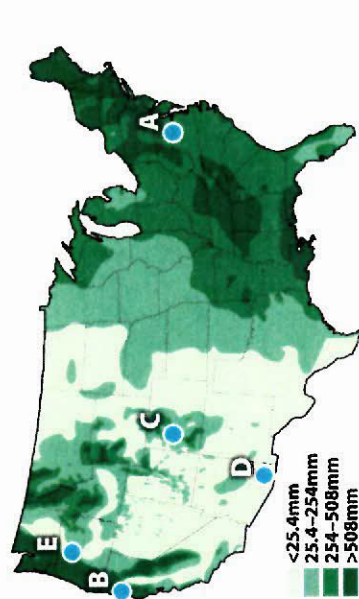


Figure 3-15. Map of annual runoff in contiguous United States showing locations of five example streams that illustrate daily runoff patterns and total annual runoff depths. (A) Rapidan River, VA; (B) Noyo River, CA; (C) Crystal River, CO; (D) San Pedro River, AZ; and (E) Metolius River, OR. All data from <http://waterdata.usgs.gov/usa/nwis/sw> (downloaded June 27, 2011). Runoff can be conceived as the difference between precipitation and evapotranspiration at the watershed scale. Varied runoff patterns in the five rivers result from divergent climate, geology, and topography.

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1 water surplus (see Section 3.2.3; Figure 3-10), when conditions for flooding are most likely to
2 exist. Typically, the occurrence of ephemeral and intermittent streams is greatest in watersheds
3 with low annual runoff and high water surplus seasonality but is also influenced by watershed
4 geologic and edaphic features (Gleeson et al., 2011).

5 Rainfall intensity can affect hydrologic connectivity in localities where watershed
6 surfaces have low infiltration capacities relative to rainfall intensities. Overland flow occurs
7 when rainfall intensities exceed watershed surface infiltration, and it can be an important
8 mechanism providing water to wetlands and river networks (Levick et al., 2008). Overland flow
9 is common at low elevations in the Southwest, due to the presence of desert soils with low
10 infiltration capacities combined with relatively high rainfall intensities (see Section 4.8). The
11 Pacific Northwest has low rainfall intensities, whereas many locations in the Mid-Atlantic,
12 Southeast, and Great Plains have higher rainfall intensities. The prevalence of impermeable
13 surfaces in urban areas can generate overland flow in virtually any setting (Booth et al., 2002).

14 River system topography and landscape form can have a profound impact on river
15 network drainage patterns, distribution of wetlands, and groundwater and surface water
16 flowpaths. Winter (2001) described six generalized hydrologic landscape forms (see
17 Figure 3-16) common throughout the United States. Mountain Valleys (see Figure 3-16A) and
18 Plateaus and High Plains (see Figure 3-16C) have constrained valleys through which streams and
19 rivers flow. The Mountain Valleys form has proportionately long steep sides with narrow to
20 nonexistent floodplains resulting in the rapid movement of water downslope. In contrast,
21 Riverine Valleys (see Figure 3-16D) have extensive floodplains that promote strong surface
22 water, hyporheic water, and alluvial groundwater connections between wetlands and rivers.
23 Small changes in water table elevations can influence the water levels and hydrologic
24 connectivity of wetlands over extensive areas in this landscape form (see Figure 3-16D). Local
25 groundwater flowpaths are especially important in Hummocky Terrain (see Figure 3-16F).
26 Constrained valleys, such as the Mountain Valley landform (see Figure 3-16A), have limited
27 opportunities for the development of floodplains and alluvial aquifers, whereas unconstrained
28 valleys, such as the Riverine Valley landform (see Figure 3-16D), provide opportunities for the
29 establishment of floodplains. River basins can be contained within a single hydrologic landscape
30 form, but larger river basins commonly comprise hydrologic landscape form complexes. For
31 example, the James River in Virginia, which flows from mountains through the Piedmont to the
32 Coastal Plain, is an example of a Mountain Valley, High Plateaus and Plains, Coastal Terrain,
33 and Riverine Valley complex.

34 Floodplain hydrologic connectivity to rivers and streams occurs primarily through
35 overbank flooding, shallow groundwater flow, and hyporheic flow (see Section 3.2).
36 Water-table depth can influence connectivity across a range of hydrologic landscape forms, but

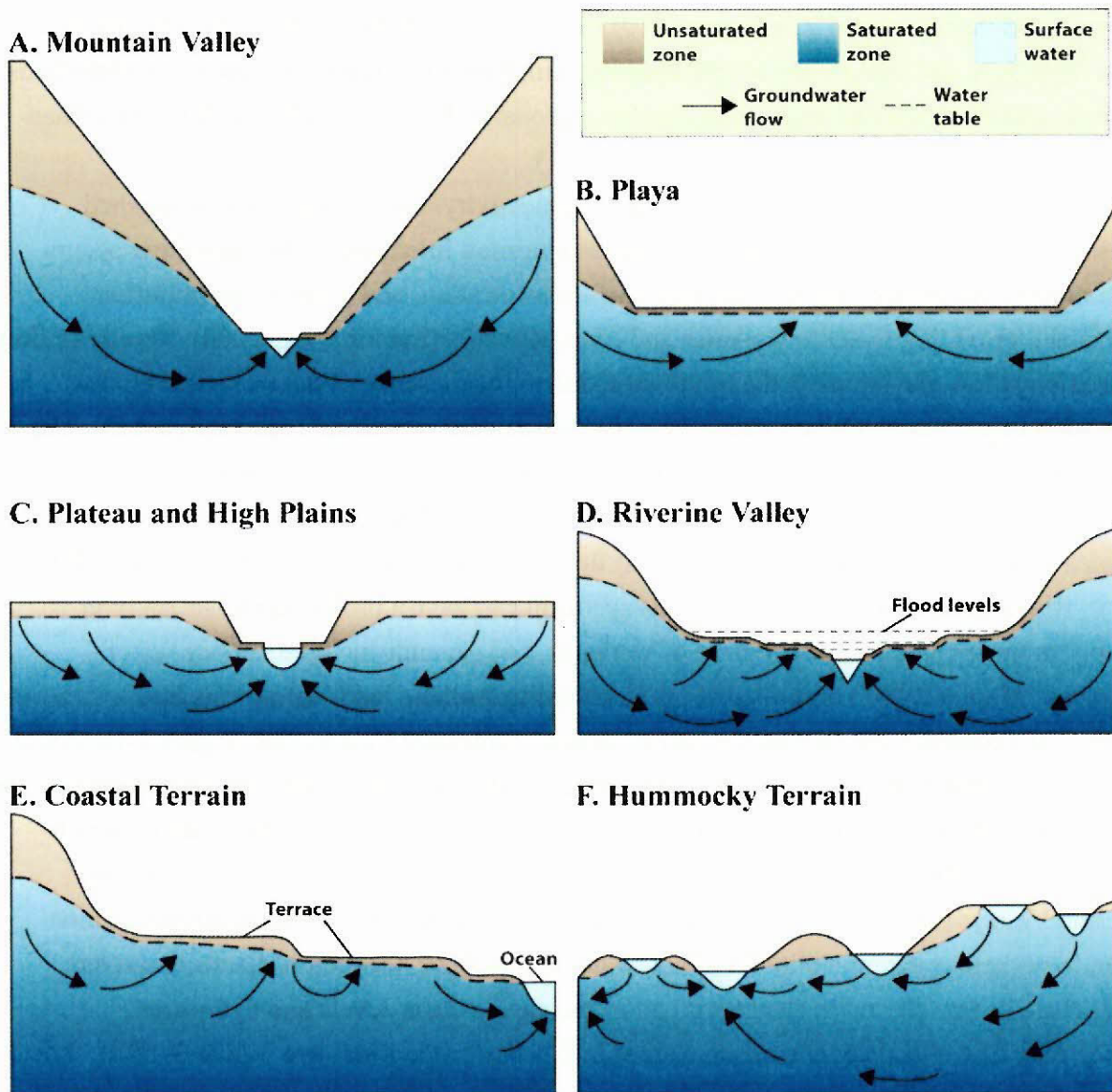


Figure 3-16. Generalized hydrologic landscape forms. (A) Mountain Valley: narrow uplands and lowlands separated by a large steep valley side; (B) Playa: large broad lowland separated from narrow uplands by steeper valleys sides (playas and basins of interior drainage); (C) Plateau and High Plains: small narrow lowlands separated from broad uplands by steeper valley sides; (D) Riverine Valley: small fundamental landscape units nested inside broader fundamental landscape unit; (E) Coastal Terrain: small fundamental landscape units nested inside broader fundamental landscape unit (coastal plain with terraces and scarps); and (F) Hummocky Terrain: small fundamental landscape units superimposed randomly on larger fundamental landscape unit. A fundamental hydrologic landscape unit is defined by land-surface form, geology, and climate.

Modified from Winter (2001).

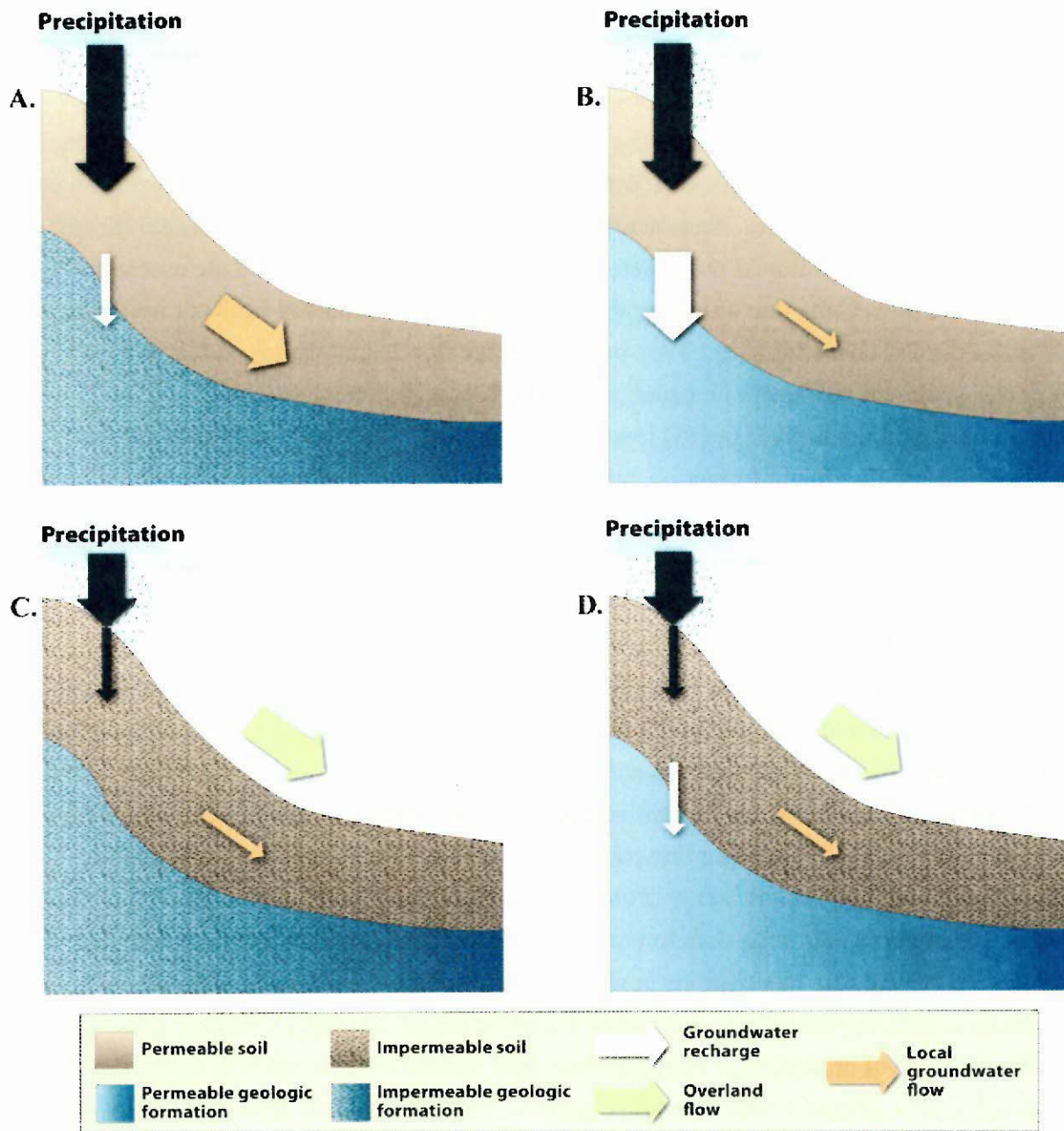


Figure 3-17. Major hydrologic flowpaths for hillslopes with combinations of permeable and impermeable soils and geologic formations. (A) Permeable soil and impermeable underlying geologic formation; (B) permeable soil and permeable underlying geologic formation; (C) impermeable soil and impermeable underlying geologic formation; and (D) impermeable soil and permeable underlying geologic formation. Width of arrow indicates relative magnitude of flow. Note that pavement can be another source of impermeable surfaces and subsequent overland flow in anthropogenically influenced settings.

1 especially in floodplains. Rivers and wetlands can shift from losing reaches (or recharge
2 wetlands) during dry conditions to gaining reaches (or discharge wetlands) during wet
3 conditions. Wet, high water-table conditions influence both groundwater and surface water
4 connectivity. When water tables are near the watershed surface, they create conditions in which
5 swales and small stream channels fill with water and flow to nearby water bodies (Wigington et
6 al., 2003; Wigington et al., 2005). Nanson and Croke (1992) noted that floodplains are formed
7 by a complex interaction of fluvial processes, but their character and evolution are essentially a
8 product of stream power (the rate of energy dissipation against the bed and banks of a river or
9 stream) and sediment characteristics. They proposed three floodplain classes based on the
10 stream power-sediment characteristic paradigm: (1) high-energy noncohesive,
11 (2) medium-energy noncohesive, and (3) low-energy cohesive. The energy term describes
12 stream power during floodplain formation, and the cohesiveness term depicts the nature of
13 material deposited in the floodplain. The cohesiveness term is also related to the hydraulic
14 properties of alluvial aquifers. Alluvium for Class 1 and 2 floodplains will tend to have higher
15 hydraulic conductivity, or a higher rate at which water moves through a saturated, permeable soil
16 or rock layer, than Class 3 floodplains. The higher the hydraulic conductivity of an alluvial
17 aquifer, the greater the exchange rate between the alluvial aquifer and river waters (Whiting and
18 Pomeranets, 1997). In addition, hyporheic and alluvial aquifer exchanges are more responsive to
19 seasonal discharge changes in floodplains with complex topography (Poole et al., 2006).

20 Within hydrologic landscape forms, soil and geologic formation permeabilities are also
21 important determinants of hydrologic flowpaths (see Figure 3-17). Permeable soils promote
22 infiltration that results in groundwater hydrologic flowpaths (see Figures 3-17A and B), whereas
23 the presence of impermeable soils with low infiltration capacities is conducive to overland flow
24 (see Figures 3-17C and D). In situations in which groundwater outflows from watersheds or
25 landscapes dominate, the fate of water depends in part on the permeability of deeper geologic
26 strata. The presence of an aquiclude near the watershed surface leads to shallow subsurface
27 flows through soil or geologic materials (see Figure 3-17A). These local groundwater flowpaths
28 connect portions of watersheds to nearby wetlands or streams (see Figure 3-3). Alternatively, if
29 a deep permeable geologic material (an aquifer) is present, water is likely to move further
30 downward within watersheds and recharge deeper aquifer (see Figure 3-17B). The permeability
31 of soils and geologic formations can both influence the range of hydrologic connectivity between
32 unidirectional wetlands and river networks. For example, a wetland that is the origin of a stream
33 can have a permanent or temporary surface water connection with downstream waters through a
34 channelized outlet (see Figure 3-18A); a wetland can be connected to downstream waters by
35 transient surface water flows through swales (see Figure 3-18B) or by shallow groundwater
36 flows (see Figure 3-18C); or a wetland can be hydrologically isolated from downstream waters

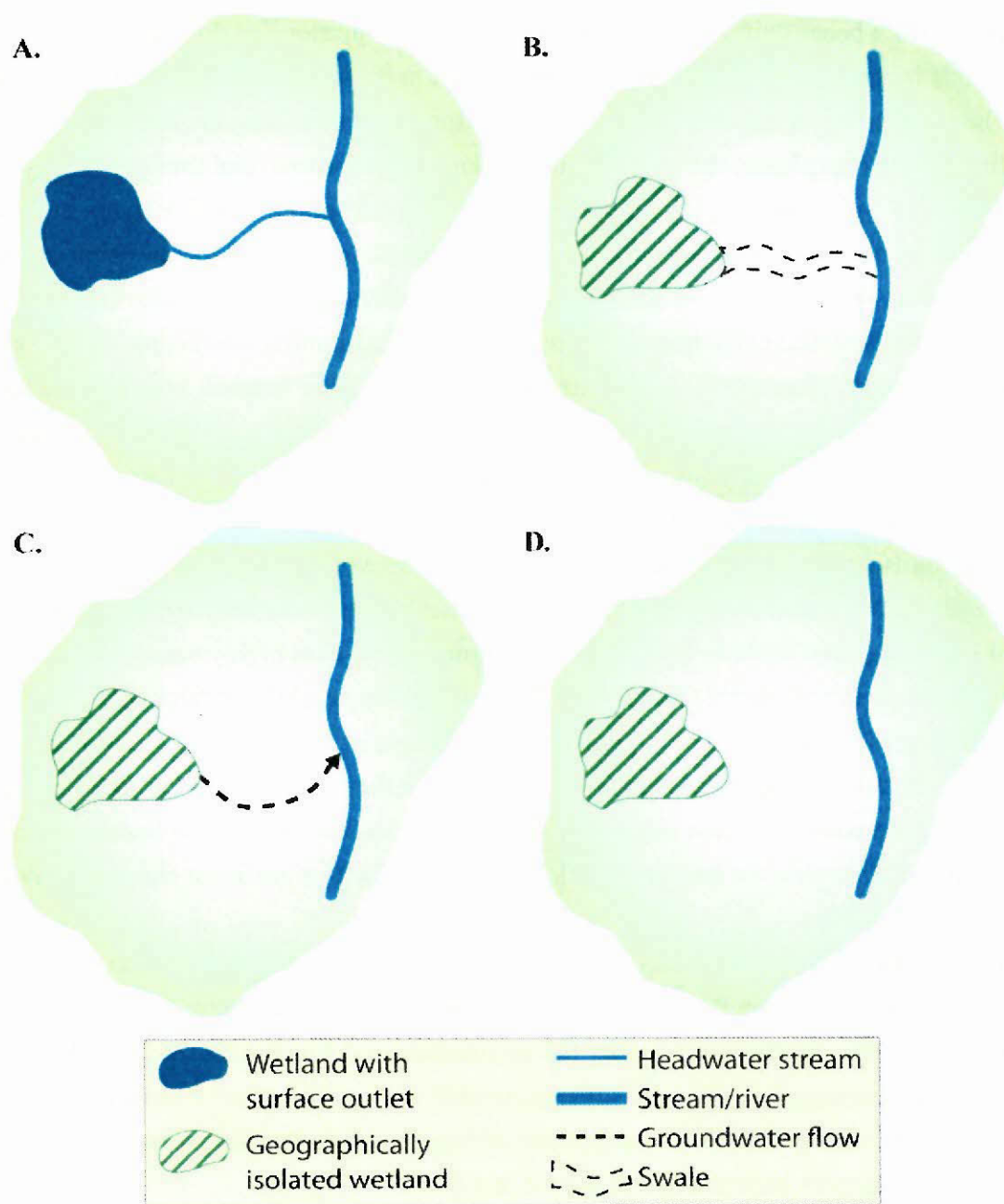


Figure 3-18. Types of hydrologic connections between unidirectional wetlands and streams or rivers. (A) Wetland connected to a river by surface flow through a headwater stream channel. (B) A wetland connected to a river by surface flow through a nonchannelized swale. Such a wetland would be considered geographically isolated if the swale did not meet the Cowardin et al. (1979) three-attribute wetland criteria. (C) A geographically isolated wetland connected to a river by groundwater flow (flowpath may be local, intermediate, or regional). (D) A geographically isolated wetland that is hydrologically isolated from a river.

Note that in A–C, flows connecting the wetland and river may be perennial, intermittent, or ephemeral.

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(see Figure 3-18D) because it recharges a deep groundwater aquifer that does not feed surface waters, or it is located in a basin where evapotranspiration is the dominant form of water loss.

The importance of climate-watershed interactions in determining the amount and seasonality of water surpluses, the timing and duration of streamflow, and thus the timing and extent of hydrologic connectivity, is illustrated by annual hydrographs for five rivers in different regions of the United States (see Figure 3-15). The hydrograph for the Rapidan River in Virginia (see Figure 3-15A) illustrates the uniform annual precipitation pattern of the East (with small variations due to increased evapotranspiration in the summer months) interacting with a steep Blue Ridge Mountain watershed that is comprised of metamorphic bedrock with alluvial and colluvial fill in the lower riparian areas (Castro and Hornberger, 1991). Hydrologic events driven by rainfall can occur anytime during the year, but are especially common in winter and spring months; these events result in expansion of the river network as ephemeral streams flow. Baseflow sustains perennial flow over a large part of the network.

Located in a region of steep slopes and impermeable bedrock (Mayer and Naman, 2011), the Noyo River drainage basin in California (see Figure 3-15B) has highly seasonal water surplus because rainfall occurs primarily from November through May and the impermeable bedrock prevents precipitation water from moving to deep groundwater. Consequently, runoff timing is similar to precipitation temporal patterns. Total runoff for the basin is high, and baseflow levels are high during the winter and low during the dry summer season. These low baseflow periods create conditions favorable for intermittent flows in streams with significant channel alluvium (Wigington et al., 2006).

The Crystal River of Colorado (see Figure 3-15C) drains a glaciated landscape in the upper portion of the Gunnison River in the Colorado Rocky Mountains. It has protracted high flow during the spring that is controlled by the accumulation and melt of snow in the basin's higher elevations during the winter and subsequent melt during spring and summer. This streamflow pattern also promotes the occurrence of intermittently flowing streams due to large water surplus differences between the high-flow and low-flow periods.

Total runoff in the San Pedro River, Arizona (see Figure 3-15D) is low and hydrologic events are commonly driven by short, intense rainstorms during the summer monsoons (Levick et al., 2008). Because a major proportion of water reaching the San Pedro River originates as overland flow to ephemeral streams that ultimately flow to the mainstem river, baseflow is limited. In other San Pedro River mainstem reaches, baseflow is supported by groundwater flow from regional and alluvial aquifers (Dickinson et al., 2010).

Like the Crystal River, the Metolius River in Oregon (see Figure 3-15E) also has snowpack in its higher elevations, but geologic conditions in the watershed alter the climate signal. Meltwaters in the Metolius River flow through long flowpaths in porous bedrock to

1 springs in or adjacent to the river (James et al., 2000; Gannett et al., 2001). Although
2 intermittent and ephemeral streams occur in the Metolius basin, most streams are spring-fed and
3 are perennial.

4 5 **3.4.2. Spatial Distribution Patterns**

6 Climate and watershed characteristics have a direct effect on spatial and temporal
7 patterns of connectivity between streams and wetlands and rivers via their effects on the timing
8 and extent of river network expansion and contraction. They also have an indirect effect by
9 influencing the spatial distribution of water bodies within a watershed (e.g., Tihansky, 1999), and
10 in particular, the spatial relationship between those water bodies and the river.

11 Hydrologic connectivity between streams and rivers can be a function of the distance
12 between the two water bodies (Bracken and Croke, 2007; Peterson et al., 2007). If channels
13 functioned as pipes, this would not be the case, and any water and its constituent materials
14 exported from a stream would eventually arrive in the river. Because streams and rivers are not
15 pipes (Bencala, 1993; see Section 3.2.3), water can be lost from the channel through
16 evapotranspiration and bank storage and diluted through downstream inputs. Thus, material
17 from a headwater stream that flowed directly into the river would be subject to less
18 transformation or dilution. On the other hand, the greater the distance a material travels between
19 a particular stream reach and the river, the greater the opportunity for that material to be altered
20 (e.g., taken up, transformed, or assimilated) in intervening stream reaches; this alteration could
21 reduce the material's direct effect on the river, but it could also allow for beneficial
22 transformations. For example, organic matter exported from a headwater stream located high in
23 a drainage network might never reach the river in its original form, instead becoming reworked
24 and incorporated into the food chain (see Figure 3-14). Similarly, higher order streams are
25 generally located closer to rivers and, therefore, can have higher connectivity than upstream
26 reaches of lower order. Note that although an individual low-order stream can have less
27 connectivity than a high-order stream, a river network has many more low-order streams, which
28 can represent a large portion of the watershed (see Section 4.2); thus, the magnitude of the
29 cumulative effect of these low-order streams can be significant.

30 The relationship between streams and the river network is a function of basin shape and
31 network configuration. Elongated basins tend to have trellis networks where relatively small
32 streams join a larger mainstem (see Figure 3-19A); compact basins tend to have dendritic
33 networks with tree-like branching, where streams gradually increase in size before joining the
34 mainstem (see Figure 3-19B). This network configuration describes the incremental
35 accumulation of drainage area along rivers, and therefore informs questions about the relative
36 contributions of streams to downstream waters. Streams in a trellis network are more likely to

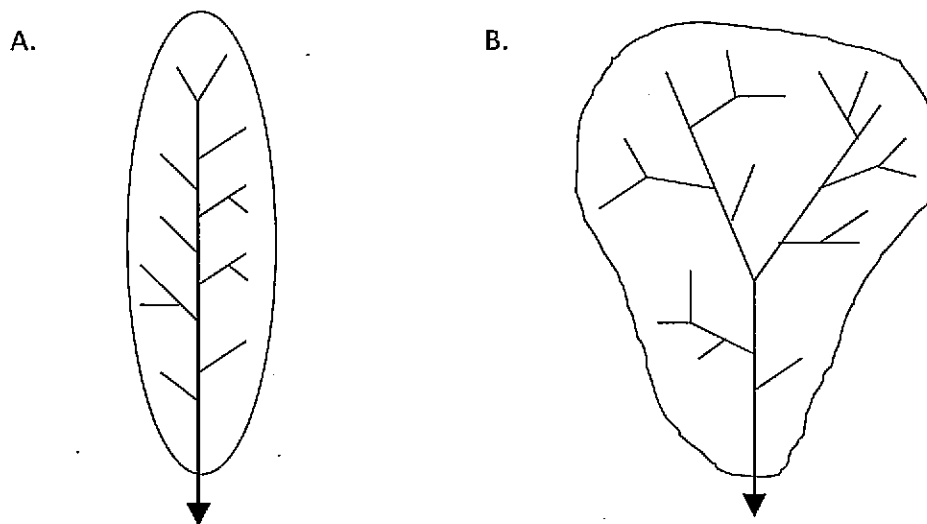
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1 connect directly to a mainstem, compared with a dendritic network. The relationship between
2 basin shape, network configuration, and connectivity, however, is complex. A mainstem in a
3 trellis network is also more likely to have a lower stream order than one in a dendritic network.
4 For example, the lower-most reach in the trellis network in Figure 3-19A is a third-order stream,
5 while that of the dendritic network (see Figure 3-19B) is a fourth-order stream.



8
9
10 **Figure 3-19. Major types of basin shapes and network configurations. (A) A**
11 **rectangular basin with trellis network, and (B) a compact basin with dendritic**
12 **network.**

13
14
15 Distance also affects connectivity between unidirectional and riparian/floodplain
16 wetlands and downstream waters. Riverine wetlands that serve as origins for lateral source
17 streams that connect directly to a mainstem river have a more direct connection to that river than
18 wetlands that serve as origins for terminal source streams high in a drainage network. This also
19 applies to riparian/floodplain wetlands that have direct surface water connections to streams or
20 rivers. If geographically isolated unidirectional wetlands have surface water outputs (e.g.,
21 depressions that experience surface water spillage or groundwater seeps; see Figure 3-18B), the
22 probability that surface water will infiltrate or be lost through evapotranspiration increases with
23 distance. For unidirectional wetlands connected through groundwater flows, less distant areas
24 are generally connected through shallower flowpaths (see Figure 3-5), assuming similar soil and
25 geologic properties. These shallower groundwater flows have the greatest interchange with
26 surface waters (see Section 3.2.2) and travel between points in the shortest amount of time.
27 While elevation is the primary factor determining areas that are inundated through overbank
28 flooding, connectivity with the river will generally be higher for riparian/floodplain wetlands

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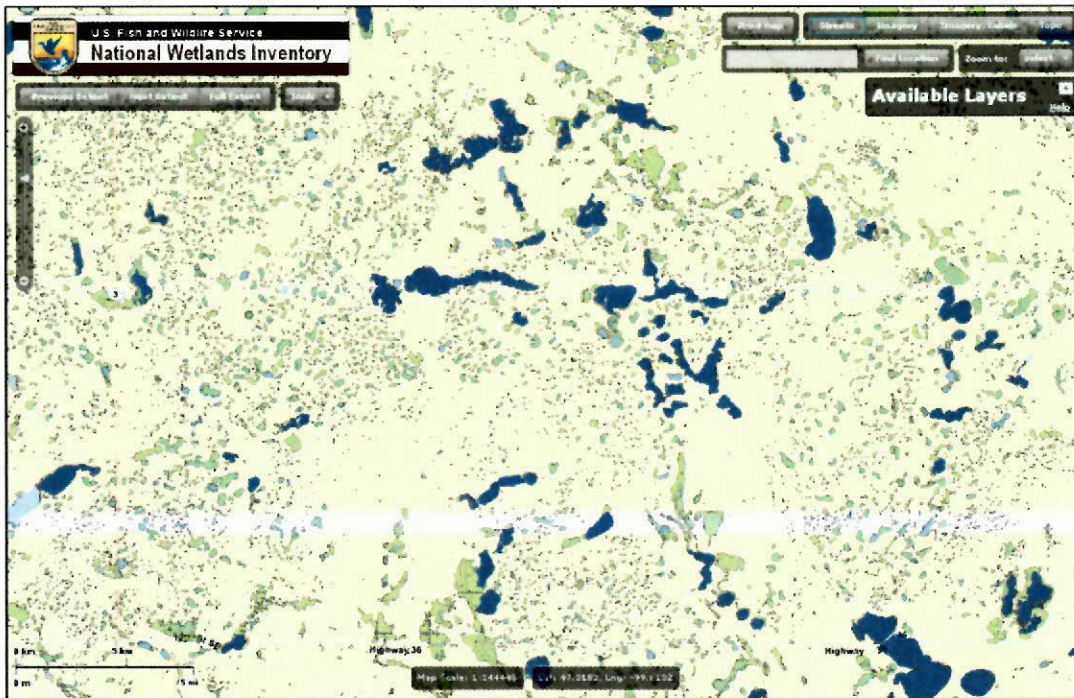
1 located near the river's edge compared with riparian/floodplain wetlands occurring near the
2 floodplain edge.

3 Biological connectivity among streams and wetlands is also influenced by distance from
4 the river network. For example, mortality of a given organism due to predators and natural
5 hazards generally increases with the distance it has to travel. The likelihood that organisms or
6 propagules traveling randomly or by diffusive mechanisms such as wind will arrive at the river
7 network decreases as distance increases.

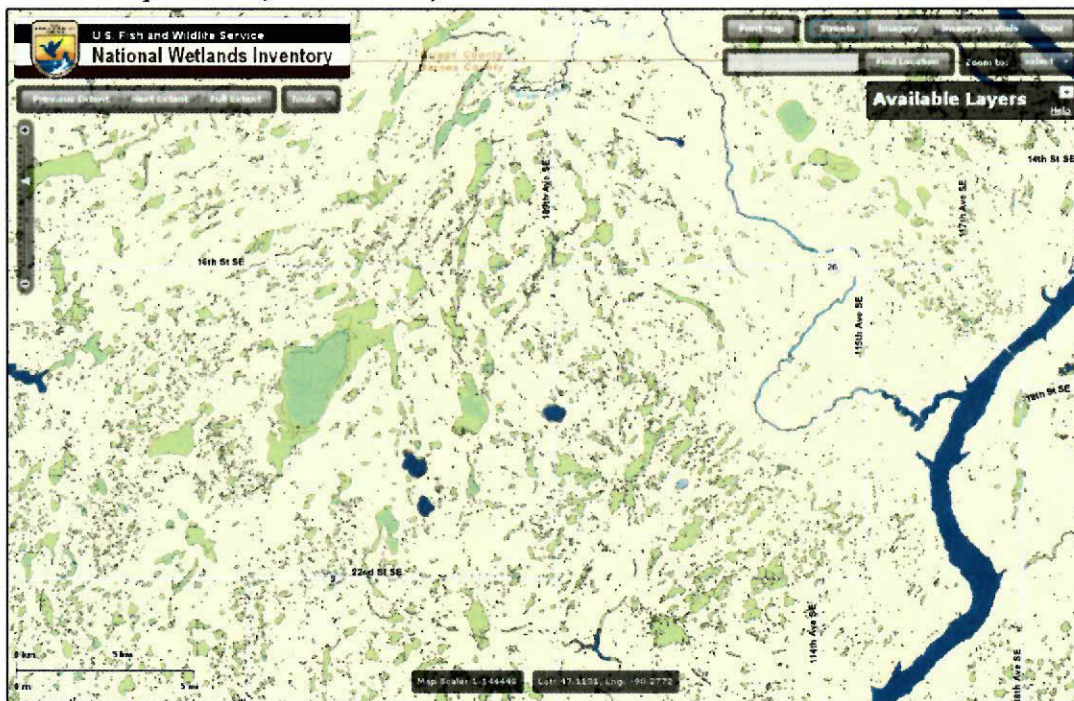
8 The distribution of distances between wetlands and river networks depends on both the
9 drainage density of the river network (the total length of stream channels per unit area) and the
10 density of wetlands. Climate and watershed characteristics influence these spatial patterns,
11 which can vary widely. For example, a subset of fens in New York State was located closer to
12 each other, on average, than a subset of Carolina bays at the Savannah River Site: the proportion
13 of wetlands located at distances of 0–100, 100–500, and >500 m was 27, 39, and 35%,
14 respectively, for the fens and 12, 44, and 44% for the Carolina bays, respectively (Bedford and
15 Godwin, 2003; Sharitz, 2003). When interpreting such distributions, however, other factors that
16 affect connectivity (e.g., differences in soils or slope) should be considered.

17 Figure 3-20 compares the spatial distribution of wetlands and streams to the river
18 network in six different landscape settings. A comparison of these figures shows landscape
19 settings ranging from no nearby streams and dense small wetlands (see Figure 3-20A), to a few
20 nearby streams with high wetland density (see Figures 3-20B and 3-20C), to less spatially
21 uniform wetlands (see Figure 3-20D), to areas with higher drainage densities and riparian (see
22 Figure 3-20E) or larger, more extensive (see Figure 3-20F) wetlands. The maps on Figure 3-20
23 represent single examples of these different settings, and so might not be representative. They
24 are useful, however, for illustrating the degree to which landscape setting can affect the
25 interspersed—and thus average distance—between wetlands and the river network, and the
26 large variability that can result. In settings with many wetlands and relatively low drainage
27 density (see Figures 3-20B, C, and D), there can be a large range in the distances between
28 individual wetlands and the stream. In contrast, areas with a higher drainage density (see Figure
29 3-20E and F) can have a narrower range of shorter distances. All things being equal, wetlands
30 with shorter distances to the stream network will have higher hydrologic and biological
31 connectivity than wetlands located farther from the same network.

A. Prairie potholes (Missouri Coteau)



B. Prairie potholes (Drift Prairie)



Wetlands			Riparian	
■ Freshwater Emergent	■ Estuarine and Marine	■ Riverine	■ Herbaceous	■ Forested/Shrub
■ Freshwater Forested/Shrub	■ Freshwater Pond	■ Other		
■ Estuarine and Marine Deepwater	■ Lake			

Figure 3-20. Examples of different landscapes showing interspersions of wetlands and streams or rivers.

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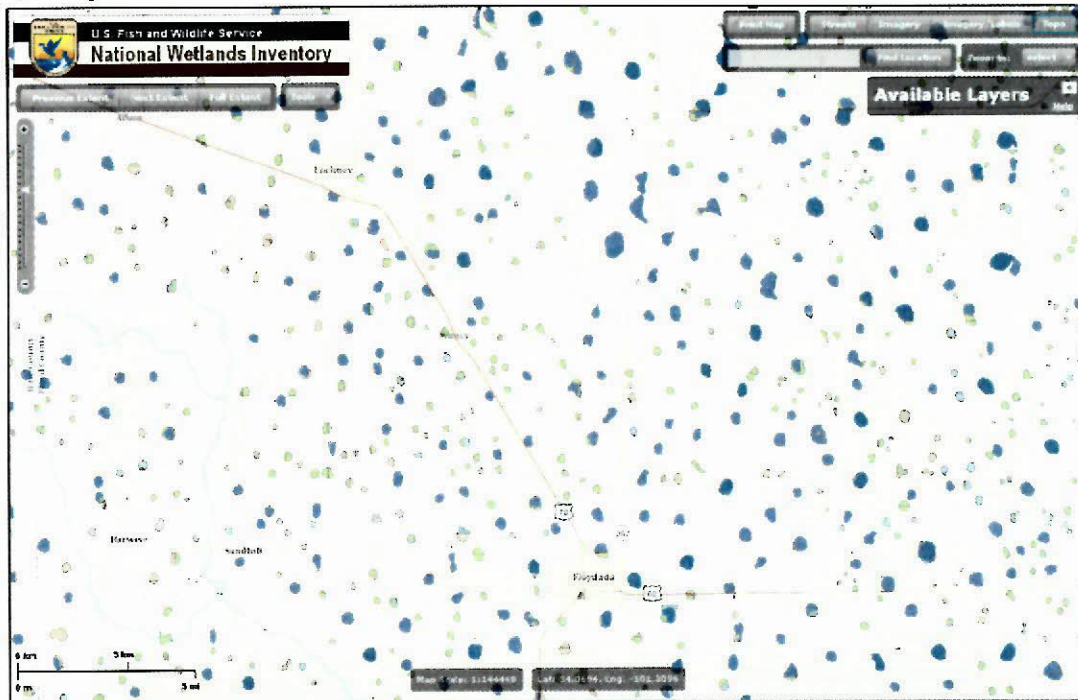
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C. Playa



D. Vernal pools

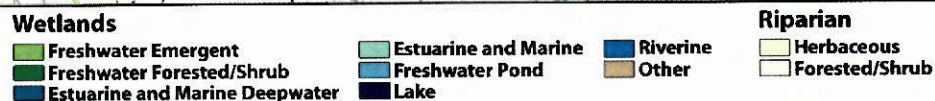
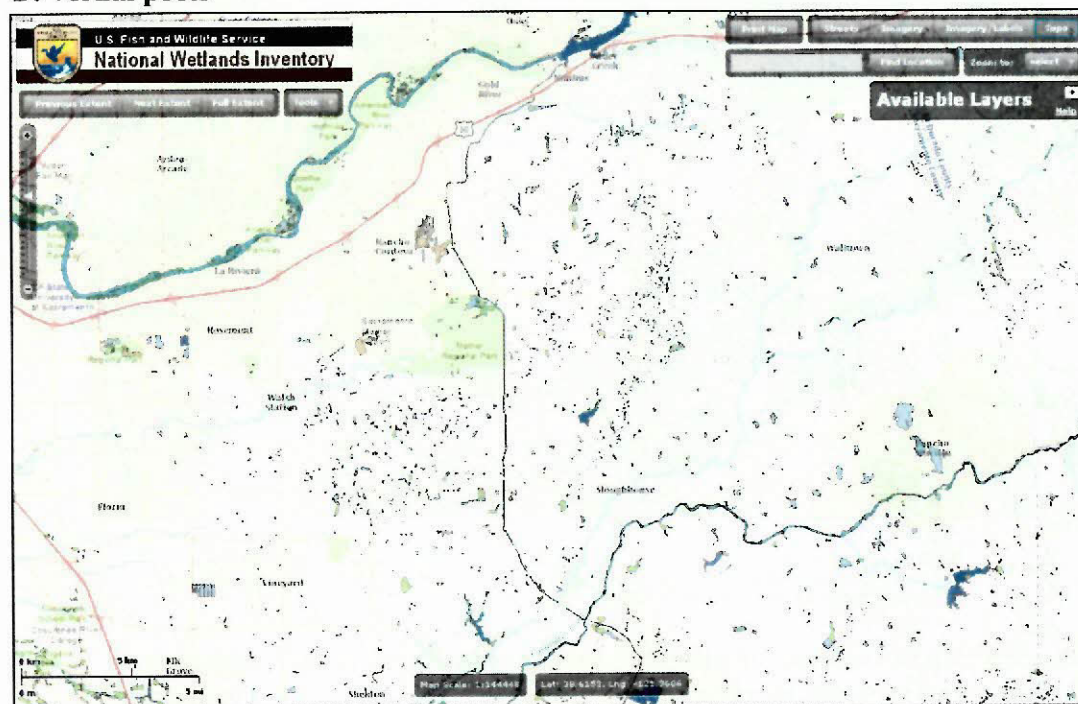


Figure 3–20. Examples of different landscapes showing interspersions of wetlands and streams or rivers (continued).

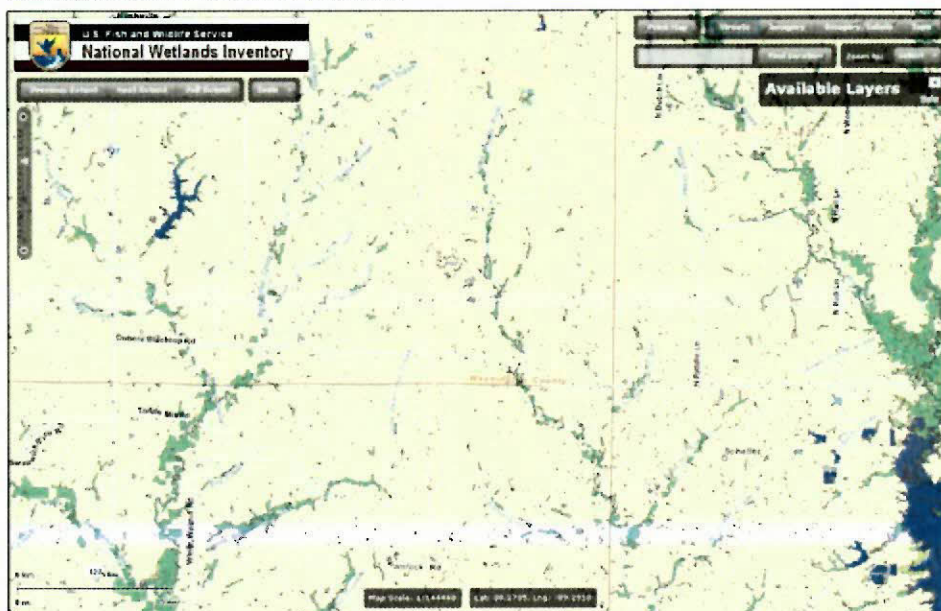
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E. Bottomland hardwood wetlands



F. Carolina bays

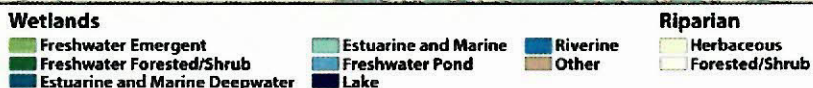
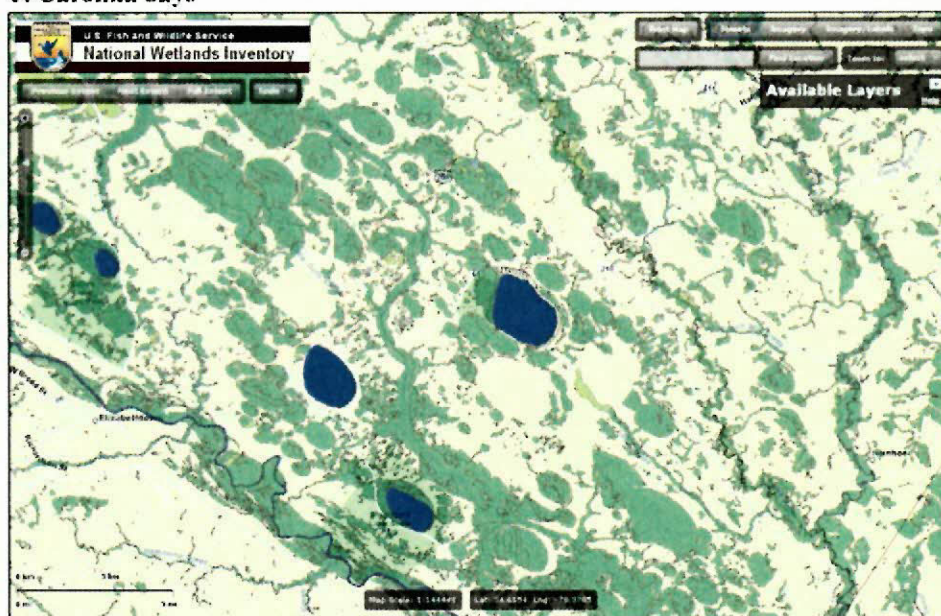


Figure 3–20. Examples of different landscapes showing interspersed wetlands and streams or rivers (continued). (A) Prairie potholes within the Missouri Coteau in North Dakota; (B) prairie potholes within the Drift Prairie in North Dakota; (C) playas in Texas; (D) vernal pools in California; (E) bottomland hardwood wetlands in Illinois; and (F) Carolina bays in North Carolina. Note all maps are at the same scale. Wetlands smaller than the minimum mapping unit (currently 0.4 ha) may not appear on maps.

Source: National Wetlands Inventory Wetlands Mapper (<http://www.fws.gov/wetlands/Data/Mapper.html>).

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3.4.3. Biota

Biological connectivity results from the interaction of physical characteristics of the environment—especially those promoting or restricting dispersal—and species' traits or behaviors, such as life-cycle requirements, dispersal ability, or responses to environmental cues. Thus, the biota within a river system are integral in determining its connectivity, and species traits that necessitate or facilitate movement of organisms or their reproductive elements tend to increase biological connectivity among water bodies.

Diadromous fauna (e.g., Pacific and Atlantic salmon, certain freshwater shrimps and snails, American eels), which require both freshwater and marine habitats over their life cycles and therefore migrate along river networks, provide one of the clearest illustrations of biological connectivity. Many of these taxa are either obligate or facultative users of headwater streams (Erman and Hawthorne, 1976; Wigington et al., 2006), meaning that they either require (obligate) or can take advantage of (facultative) these habitats; these taxa thereby create a biological connection along the entire length of the river network. For example, many Pacific salmon species spawn in headwater streams, where their young grow for a year or more before migrating downstream, living their adult life stages in the ocean, and then migrating back upstream to spawn. Many taxa can also exploit temporary hydrologic connections between rivers and floodplain wetland habitats, moving into these wetlands to feed, reproduce, or avoid harsh environmental conditions and then returning to the river network (Copp, 1989; Junk et al., 1989; Smock, 1994; Richardson et al., 2005).

Biological connectivity does not solely depend on diadromy, however, as many nondiadromous organisms are capable of significant movement within river networks. For example, organisms such as pelagic-spawning fish and mussels release eggs or larvae that disperse downstream with water flow (e.g., Platania and Altenbach, 1998; Schwalb et al., 2010); many fish swim significant distances both upstream and downstream (e.g., Gorman, 1986; Hitt and Angermeier, 2008); and many aquatic macroinvertebrates actively or passively drift downstream (e.g., Elliott, 1971; Müller, 1982; Brittain and Eikeland, 1988; Elliott, 2003). Taxa capable of movement over land, via either passive transport (e.g., wind dispersal or attachment to animals capable of terrestrial dispersal) or active movement (e.g., terrestrial dispersal or aerial dispersal of winged adult stages), can establish biotic linkages between river networks and wetlands, as well as linkages across neighboring river systems (Hughes et al., 2009).

3.4.4. Human Activities and Alterations

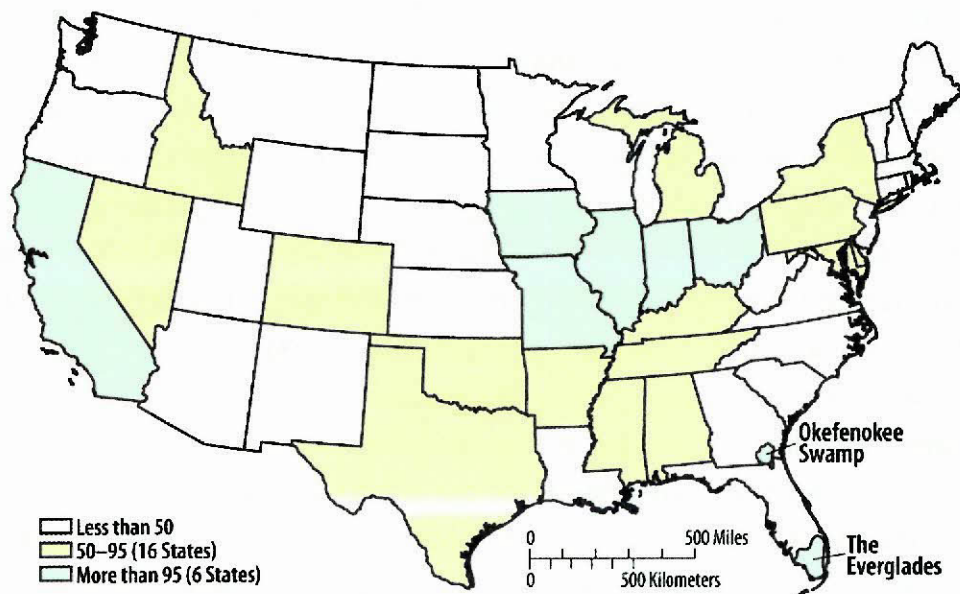
Human activities frequently alter connectivity between headwater streams, riparian/floodplain wetlands, unidirectional wetlands, and downgradient river networks, thereby

1 altering the transfer and movement of materials and energy between river system components.
2 In fact, the individual or cumulative effects of headwater streams and wetlands on river networks
3 often only become discernible following human-mediated changes in degree of connectivity.
4 These human-mediated changes can result in increased or decreased hydrologic and biological
5 connectivity (or, alternatively, decreased or increased hydrologic and biological isolation). For
6 example, activities and alterations such as dams, levees, water abstraction, and piping,
7 channelization, and burial can reduce hydrologic connectivity between streams and wetlands and
8 rivers, whereas activities and alterations such as wetland drainage, irrigation, impervious
9 surfaces, interbasin transfers, and channelization can enhance hydrological connections.
10 Biological connectivity can be affected similarly: for example, dams and impoundments might
11 impede biotic movement, whereas nonnative species introductions artificially increase biotic
12 movement. Further complicating the issue is that a given activity or alteration might
13 simultaneously increase and decrease connectivity, depending on which part of the river network
14 is considered. For example, channelization and levee construction reduce lateral expansion of
15 the river network (thereby reducing hydrologic connections with floodplains), but might increase
16 this connectivity downstream due to increased magnitude and frequency of high flows.

17 To illustrate, we describe two notable alterations that affect river system connectivity:
18 dams (and their associated impoundments) and wetland drainage. The United States has more
19 than 80,000 dams, over 6,000 of which exceed 15 m in height (USACE, 2009). Numerous
20 studies have shown that dams impede biotic movements, reduce biological connectivity between
21 upstream and downstream locations (e.g., Greathouse et al., 2006; Hall et al., 2011), and form a
22 discontinuity in the normal stream-order related progression in stream ecosystem structure and
23 function (Stanford and Ward, 1982). Upstream of large dams, riparian areas are permanently
24 inundated, increasing lateral hydrologic connectivity. Downstream, dams decrease peak stream
25 volumes during the normal high runoff seasons, while increasing minimum flows during normal
26 low-flow seasons—an overall dampening of stream-flow variability (Poff et al., 2007). Because
27 many riverine organisms are adapted (life history, behavioral, and morphological) to the
28 seasonality of natural flow regimes, dampening flow variability can have deleterious effects on
29 species persistence where dams have been built (Lytle and Poff., 2004). This reduction in high
30 flows also decreases the connectivity of riparian wetlands with the stream by reducing the
31 potential for overbank lateral flow. This can affect downstream water quality, because overbank
32 flow deposits sediment and nutrients that would otherwise remain entrained in the river (Hupp et
33 al., 2009).

34 The greatest human impact on riparian/floodplain wetlands and unidirectional wetlands
35 has been through wetland drainage (see Figure 3-21), primarily for agricultural purposes.
36 Estimates show that the conterminous United States have lost more than 50% of their original

A. Percent of Wetlands Lost, 1780s–1980s



B. Artificially Drained Agricultural Land, 1985 (1 dot = 8100 ha)

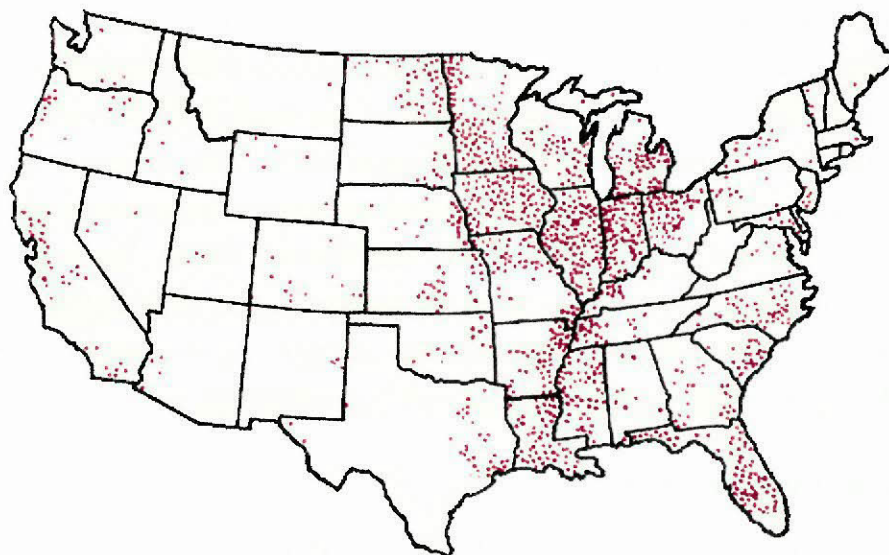


Figure 3-21. Comparison of percent wetland loss between (A) the 1780s and mid-1980s with (B) the distribution of artificially drained agricultural land in 1985. One dot equals 8100 ha.

From Blann et al. (2009), as modified from Dahl (1990).

wetlands, with some states losing more than 90%; wetland surface areas also have declined significantly (Dahl, 1990).

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1 Drainage causes a direct loss of function and connectivity in cases where wetland
2 characteristics are completely lost. Wetland drainage, however, also increases hydrologic
3 connectivity between the landscape—including drained areas that retain wetland
4 characteristics—and downstream waters. Effects of this enhanced hydrologic connectivity
5 include (1) reduced water storage and more rapid conveyance of water to the network, with
6 subsequent increases in total runoff, baseflows, stormflows, and flooding risk (Wiskow and van
7 der Ploeg, 2003; Blann et al., 2009); (2) increased delivery of sediment and pollutants to
8 downstream waters; and (3) increased transport of water-dispersing organisms (Babbitt and
9 Tanner, 2000; Baber et al., 2002; Mulhouse and Galatowitsch, 2003). Biological connectivity,
10 however, also can decrease with drainage and ditching, as average distances between wetlands
11 increase and limit the ability of organisms to disperse between systems aerially or terrestrially
12 (Leibowitz, 2003). Groundwater withdrawal also can affect wetland connectivity by reducing
13 the number of wetlands. Of particular concern in the arid Southwest is that groundwater
14 withdrawal can decrease regional and local water tables, reducing or altogether eliminating
15 groundwater-dependent wetlands (Patten et al., 2008). However, groundwater withdrawal also
16 can increase connectivity in areas where that groundwater is applied or consumed.

17 Particularly noteworthy is that restoration of hydrologic connectivity, particularly in
18 systems with widespread human alterations, also might adversely affect downstream waters
19 (Jackson and Pringle, 2010). For example, dam removal can result in the downstream transport
20 of previously sequestered pollutants (Jackson and Pringle, 2010); dam releases to restore flows,
21 without simultaneous restoration of sediment supplies, can result in downstream channel
22 degradation (Germanoski and Ritter, 1988; Schmidt and Wilcock, 2008). Hammersmark et al.
23 (2008) used a modeling study to show how the restoration of incised stream channels can
24 improve connectivity between streams and floodplains and thus restore predisturbance hydrology
25 (i.e., increased floodplain water storage, reduced peak stormflow, and reduced baseflow).

26 27 **3.4.5. Interactions Among Factors**

28 Interactions among the factors discussed above can be complex. Here we provide an
29 example of temporary surface water connections between wetlands in the prairie pothole region
30 (PPR) to illustrate these complex interactions (Leibowitz and Vining, 2003). Further details on
31 wetlands in the PPR are provided in Section 5.8.

32 During high water conditions in 1995, a temporary surface water connection was
33 observed between two geographically isolated prairie potholes in the region's Drift Prairie.
34 Based on a spatial analysis during similarly wet conditions in 1996, 28% of the wetlands in a
35 40 km² area containing the sites had a temporary surface water connection to at least one other

wetland. This included a complex (defined in the study as a group of wetlands interconnected through temporary surface water connections) of 14 wetlands.

In considering these findings, Leibowitz and Vining (2003) suggested that precipitation and local relief are the primary factors controlling the spatial distribution of these temporary surface connections. Precipitation is the ultimate source of water that fills these wetlands, whereas relief controls how much the water level in a wetland must rise before spillage occurs (water level is also influenced by evapotranspiration and groundwater, but groundwater dynamics are difficult to predict for individual wetlands). Relief also controls mixing—which could occur in flatter areas when the boundaries of expanding wetlands overlap—by determining the change in surface area per change in water level. Thus, for a given level of precipitation, the number of surface connections occurring between wetlands should be inversely proportional to local relief. Within the PPR, precipitation generally decreases from east to west, while relief generally increases. The easternmost physiographic region in the PPR is the Red River Valley, a relatively flat ancient lakebed (Lake Agassiz) having deep deposits of silt and clay. Water can pond easily on these deposits, producing shallow wetlands and integrated drainage (i.e., the presence of stream networks). The Missouri Coteau, which forms the western boundary of the PPR, consists of dead-ice glacial moraine. This area has hummocky terrain, and local relief can be as great as 15–45 m in steeper areas (Winter et al., 1998). As a result, the Coteau has deeper wetlands and little to no integrated drainage. The Drift Prairie, located between the Red River Valley and the Missouri Coteau, is an undulating plain formed on ground moraine. Relief, wetland depth, and the level of integrated drainage in the Drift Prairie are intermediate in comparison with the other two regions.

Leibowitz and Vining (2003) hypothesized that the combined effect of these patterns in precipitation and relief should produce a strong east-west gradient across the PPR in the occurrence of intermittent surface-water connections. Both the absolute number of connections and complex size (the number of wetlands contained in a complex) should be highest in the Red River Valley. Given the relative flatness of this area, mixing should be the more common mechanism for temporary connections. The number of temporary connections and complex size should be lower in the Drift Prairie, and spillage might dominate in this hillier terrain. In the Missouri Coteau, where relief is greatest, the occurrence of these temporary connections should be rare and limited to small complex sizes. Human impacts, however, could affect these trends (see Section 3.4.4).

Beyond these regional trends in relief and precipitation, local variation in the occurrence of intermittent surface-water connections should be influenced strongly by groundwater dynamics. The groundwater hydrology of prairie potholes has been well investigated at several sites (e.g., Winter et al., 1998; Winter and Rosenberry, 1998). However, the specific

1 groundwater interactions—and hence the effects of groundwater movement on spillage or
2 mixing—are unknown for most prairie potholes. It would generally be expected that, all else
3 being equal, groundwater discharge wetlands should receive more water, and so have a higher
4 probability of spillage, than groundwater recharge wetlands, since recharge should reduce the
5 amount of water available for spillage.

6 A major factor influencing the temporal distribution of intermittent connections within
7 the PPR is wet-dry cycles. These cycles are driven by climatic changes that have occurred
8 throughout the Holocene. For example, there is evidence of 20-, 22-, 50-, 100-, and 200-year
9 climatic cycles (Ashworth, 1999). Wetland hydrology responds dramatically to these wet-dry
10 cycles as groundwater levels and precipitation patterns fluctuate. In 1996, the average monthly
11 Palmer Hydrological Drought Index for central North Dakota was 4.02 (88th percentile),
12 compared with a median of 1.00 for annually calculated monthly averages between 1895 and
13 2001. Moisture levels of this magnitude—and consequently the degree of connectivity observed
14 (Leibowitz and Vining, 2003)—would be expected to occur during wetter portions of wet-dry
15 cycles.
16

4. STREAMS: PHYSICAL, CHEMICAL, AND BIOLOGICAL CONNECTIONS TO RIVERS

4.1. ABSTRACT

The physical structure of a river network inherently demonstrates connectivity between all streams and their downstream rivers. Substantial evidence supports physical, chemical, and biological connections from headwater streams—including those with ephemeral, intermittent, and perennial flows—to waters immediately downstream through transport of water and associated materials, as well as movement of organisms and reproductive propagules, and bidirectional geomorphic adjustments. Among the most compelling evidence for the effects of headwater streams on rivers is as sources of water, nitrogen, organic carbon, and contaminated sediment; as sinks of nitrogen, carbon, and contaminants; and as providers of essential habitat for migratory animals such as anadromous salmon. Small streams as a class provide substantial quantities of water to larger water bodies. For example, first-order streams contribute approximately 60% of the total mean annual flow to all northeastern U.S. streams and rivers. Infrequent, high-magnitude events are especially important for transmitting materials from headwater streams in most river networks. The strongest lines of evidence supporting the effects of headwater streams are from basins where headwater streams drain a unique (in terms of hydrology, geology, human alteration) portion of the basin. Our examination of the literature makes clear that investigation of connections among river network components continues to be an active area of scientific research. Additional empirical data and further breakthroughs in our ability to quantify linkages across large spatio-temporal scales will continue to enhance our understanding of the complexity of river networks.

4.2. INTRODUCTION

The purpose of this chapter is to describe the state of knowledge of stream connectivity and its effects on the physical, chemical, and biological condition of downstream waters. Although we recognize that streams also are important sources of water and other materials to nearby terrestrial and groundwater systems (e.g., Gray, 1993; Shentsis and Rosenthal, 2003; Walters et al., 2008), we focus here on surface water connections between streams and rivers, as well as subsurface water interactions integral to surface water connections and downstream water condition. The evidence primarily focuses on the downstream connections of small (headwater) streams to downstream waters, but some evidence is drawn from connections of larger streams to rivers, reservoirs, lakes, and coastal waters. We consider the peer-reviewed evidence for connectivity and its effects on downstream rivers in terms of physical (see Section 4.3), chemical (see Section 4.4), and biological (see Section 4.5) connections between upstream and

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1 downstream habitats. While recognizing that many linkages between streams and downstream
2 waters cross physical, chemical, and biological boundaries, we have chosen this format for ease
3 of presentation. We close this general section on stream-river connections with a synthesis of the
4 evidence in terms of the conceptual framework (see Section 4.6), and then consider in greater
5 detail the evidence for connectivity in two specific stream types: prairie streams (see Section 4.7)
6 and arid streams of the Southwest (see Section 4.8). Prairie streams and arid streams of the
7 Southwest were selected for case studies in part because a high proportion of these river
8 networks are composed of intermittent and ephemeral streams.

9 Streams range greatly in size in terms of both drainage area and discharge, and generally,
10 their abundance is inversely related to their size. First-order streams typically are most abundant,
11 although individually they have the smallest drainage areas and shortest average stream lengths
12 (Horton, 1945; Schumm, 1956; Ijjasz-Vasquez et al., 1993). When drainage area and stream
13 length of headwater streams are combined, however, they can represent most of the river
14 catchment and network.

15 The contribution of headwater streams to river networks in terms of stream number,
16 length, or drainage area over large geographic regions has been difficult to determine, even with
17 advances in remote sensing and geographic information systems (GIS). The small size of
18 headwater streams makes distinguishing them from surrounding areas and overlying tree
19 canopies in most regions difficult (Gilvear and Bryant, 2003). Numerous studies have shown
20 that existing U.S. hydrographic databases and topographic maps underestimate the extent of
21 headwater streams (Morisawa, 1957; Gregory, 1976; Hansen, 2001; Heine et al., 2004; Stoddard
22 et al., 2005; Colson et al., 2008; Roy et al., 2009). Therefore, most first-order streams portrayed
23 on databases and maps are second- or third-order streams when ground truthed. For example,
24 over 80% of mapped (1:25,000 scale topographic maps) stream terminuses in a Massachusetts
25 watershed that were surveyed underestimated the upstream extent of the channels (Brooks and
26 Colburn, 2011). On average these unmapped upstream segments were nearly 0.5 km in length
27 and 40% had one or more upstream tributaries (Brooks and Colburn, 2011). Despite the widely
28 known underestimation by databases and maps, first-order streams recognized by the U.S.
29 Geological Survey (USGS) medium-resolution (1:100,000-scale) National Hydrographic
30 Database (NHD) represented 53% (2,900,000 km) of total stream length (Nadeau and Rains,
31 2007b). Moreover, approximately 50% of these first-order streams were classified as not having
32 year-round flow (i.e., nonperennial; Nadeau and Rains, 2007b; see Section 3.2.2). Because most
33 databases and maps do not portray the true extent of headwater and nonperennial streams, these
34 resources do not accurately reflect the true geomorphic definition of stream order and should not
35 be used to define the upper extent of what is and is not a stream within a watershed.
36 Nevertheless, given what we do know from hydrographic databases and about the distribution of

streams by size, it is clear that headwater and nonperennial streams represent a large fraction of river networks in the United States.

In the following sections, we consider connectivity between streams and downstream rivers in terms of the physical, chemical, and biological connections between them. These types of connections are not independent, however. For example, the physical connection of water flow through the river network largely forms the foundation for chemical and biological connections. The scientific community is increasingly aware that integration across multiple disciplines is fundamental to obtaining deeper understanding, and riverine science is no exception (Paola et al., 2006; Wood et al., 2007; Thorp et al., 2008).

4.3. PHYSICAL CONNECTIONS

Physical connections result from the transport of nonliving materials that do not chemically change (or change slowly) from streams to downstream rivers. In this section we discuss factors controlling water, temperature (or heat energy), sediment, and wood in streams; how these materials are transported downstream; and evidence that these connections affect the condition of downstream rivers.

4.3.1. Water

The recurrent, concentrated surface flow of water from surface runoff and groundwater develops and maintains river networks, and water is the primary medium carrying other materials from streams to rivers (see Section 3.3). Most (although not all) rivers receive most of their water from tributaries rather than through direct precipitation on or groundwater input to river segments (Winter, 2007; Bukaveckas, 2009). Alexander et al. (2007) modeled flow through stream networks in the northeastern United States and estimated that first-order streams (designated on the 1:100,000-scale NHD river network) provide approximately 70% of the mean annual water volume in second-order streams and about 55% and 40% of the mean water volume in fourth- and higher order rivers, respectively. Overall, first-order streams contribute about 60% of the total volume of mean annual flow to all northeastern streams (Alexander et al., 2007). Contributions of headwaters to downstream baseflow vary among river networks, depending on large-scale factors (see Section 3.4). For example, headwater streams which have stronger connections to groundwater or which consistently receive more precipitation, relative to downstream reaches, will have a larger effect on river baseflows. Hydrologic data from 11 nested gages distributed throughout a 176 km²-basin in the Catskill Mountains, NY were used to assess the extent of spatial correlation in baseflow discharge (Shaman et al., 2004). Baseflow discharge in smaller streams (i.e., with watersheds <8 km²) was more weakly correlated with

1 mainstem discharge than discharge in larger streams; the authors concluded that this pattern
2 reflected greater contributions by deep groundwater as drainage area increased (Shaman et al.,
3 2004). Using geochemical tracers and hydrologic data from 32 nested stations in a
4 1,849 km²-basin of the River Dee in Scotland, Tetzlaff and Soulsby (2008) determined that
5 streams draining the upper 54% of the catchment contributed 71% of baseflow. This finding is
6 particularly significant because the upper catchment received only 58% of the total annual
7 precipitation, indicating that groundwater storage in the headwater catchments was important in
8 maintaining downstream baseflows (Tetzlaff and Soulsby, 2008). In contrast, headwater streams
9 (0.11–3.5 km²) making up 33% of the total area in a northern Sweden basin (78 km²) contributed
10 only 18% of the summer baseflow at the basin outlet (Temnerud et al., 2007). The specific
11 discharge contribution (L s⁻¹ km²) for headwater streams, however, varied by an order of
12 magnitude (~0.5–8.0) reflecting the heterogeneity (i.e., mires, lakes, forest) of the study
13 catchment (Temnerud et al., 2007).

14 The role of headwater streams also can be inferred from variation in river hydrologic
15 response over space. Discharge increases with drainage area, and the general assumption is that
16 they have a positive relationship such that drainage area is a common proxy for discharge. The
17 relationship can be written as $Q = kA^c$, where Q is discharge (m³ s⁻¹), k is a constant representing
18 hydrologic factors such as antecedent moisture and precipitation, A is drainage area (km²), and c
19 is the scaling power constant. This scaling power reflects how the rate of discharge increases
20 with drainage area and can be useful for qualitatively assessing the contributions of headwaters
21 to downstream discharge. Where $c \approx 1$, discharge is generated proportionally with increasing
22 drainage area; where $c < 1$, upstream portions of the catchment (where small streams tend to be
23 most abundant) generate more discharge per unit area than downstream portions; where $c > 1$,
24 downstream portions generate more discharge per area than upstream reaches. Data from
25 multiple USGS gages along large, unregulated rivers showed that mean and peak annual
26 discharge does not always increase proportionally with drainage area (Galster, 2007, 2009). Of
27 the 40 rivers examined, only 16 had linear peak annual discharge-area relationships ($c \approx 1$)
28 throughout their period of record (Galster, 2009). Eleven rivers had relationships where $c < 1$,
29 three rivers had relationships where $c > 1$, and ten showed changes in the relationship over their
30 period of record. Rivers having $c < 1$ suggests that these rivers derive a higher proportion of
31 their flow from headwater streams. Rivers having $c > 1$ suggests that the upstream portions
32 might store more water per unit area than downstream areas. In some cases, however,
33 urbanization in the lower portions of the catchment can cause greater flow generation per unit
34 area, leading to a similar relationship (Galster et al., 2006).

35 Despite the variability in area-discharge relationships, most watersheds have a value of c
36 between 0.8 and 1 (Galster, 2007), suggesting that to a first approximation, drainage area can be

1 used to estimate the proportion of flow that arises from headwater streams. For example,
2 Alexander et al. (2007) found that the catchments of first-order streams accounted for 57% of the
3 total drainage area, and 55% of the total annual river flow of the New England states. Caruso
4 and Haynes (2011) reported that first-order catchments made up 61% of the total drainage area
5 of the Upper Colorado River basin. In this case, however, the first-order streams produced a
6 lower proportion (41%) of the total annual river flow than suggested by their total drainage area,
7 explained in part by the fact that 84% of the streams were intermittent. Both studies used the
8 1:100,000-scale NHD, in which first-order catchments generally correspond to second-order
9 catchments at the 1:24,000 scale (Alexander et al., 2007). These results, representing two very
10 different parts of the United States, strongly suggest that headwater streams, even where
11 seasonally dry, generate a large fraction of the nation's stream and river flows.

12 The propagation of stormflow through river networks provides clear evidence supporting
13 the existence of hydrologic connectivity between headwater streams and rivers, particularly
14 when an intense storm occurs over only the headwater portions of a river network. In these
15 cases, the hydrograph peaks sharply in the headwater streams, indicating a quick response to
16 precipitation (see Figures 3-8 and 3-11). Timing of the storm and onset of the peak will be
17 increasingly delayed with increasing distance down the network (see Figure 3-11 and further
18 discussion on hydrologic dispersion below). Typically, discharge magnitude increases as
19 stormflow accumulates incrementally over the stream network (Allan, 1995). The contribution
20 of tributaries to rivers during widespread floods manifests as stepped increases in discharge
21 immediately below confluences, as water flows through a river network (see Figure 4-1).

22 Such propagation was recorded following a monsoonal storm event through an arid
23 network of ephemeral channels in the Río Grande, NM (see Figure 4-2). The high intensity
24 storm dropped approximately 18–25% of the annual rainfall over a 2-day period on the stream's
25 approximately 16,000-km² drainage area. Discharge recorded at two gages on the stream and
26 three gages on the Rio Grande downstream of the confluence illustrated lag time and peak
27 hydrograph broadening at least 127 km downstream (Vivoni et al., 2006). The contributions of
28 the stormflow from the ephemeral stream accounted for 76% of the flow at the Rio Grande,
29 despite being considered to have a flood return interval only ranging from 1.11 to 1.84 years
30 across the USGS gages in the network (Vivoni et al., 2006).

31 Here we describe how water flowing through the streams in river networks shapes the
32 hydrologic response (time to peak flow, peak flow magnitude, and recession of peak flow) in
33 downstream rivers (see also Section 3.2). A key effect streams have in a network structure on
34 the hydrologic response is dispersion, or the spreading of water output from a drainage basin
35 over time. Hydrologic dispersion is the combined effect of several mechanisms across spatial

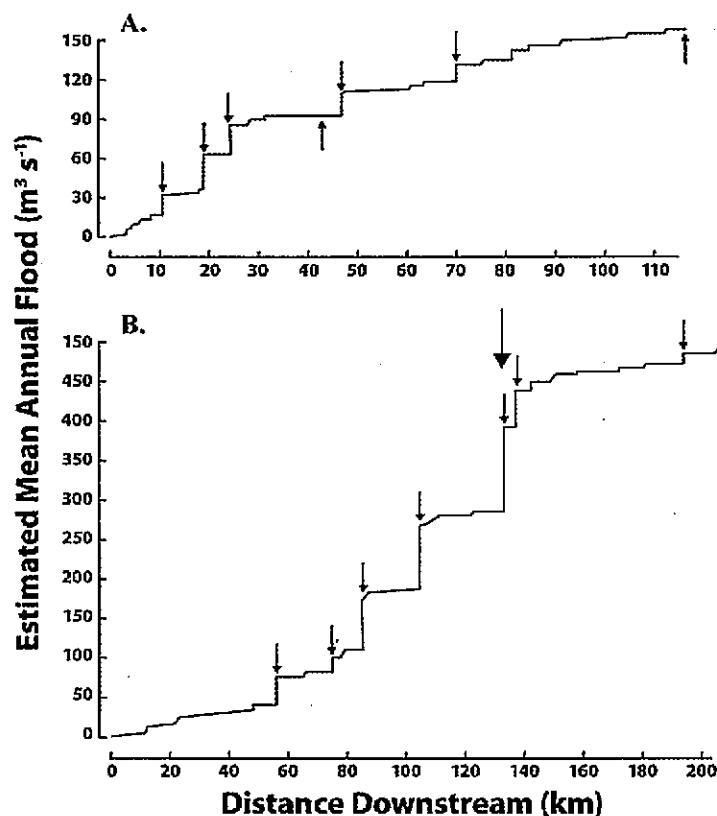


Figure 4-1. Longitudinal pattern of flow along (A) River Derwent and (B) River Trent, illustrating stepped increases in flow associated with contributions from tributaries. Small arrows indicate location of tributary confluences along the mainstem; bold arrow in (B) indicates the confluence of the two rivers.

Modified from Knighton (1998).

scales that influence the travel time and volume of water reaching a river network outlet (Saco and Kumar, 2002).

The components of hydrologic dispersion most relevant to river networks include **hydrodynamic dispersion**, **geomorphologic dispersion**, and **kinematic dispersion**. At the scale of individual channels within the network, hydrodynamic dispersion represents storage, turbulence, and shear stress processes that make portions of a channel's volume move downstream faster than others, rather than as a discrete pulse. Hydrodynamic dispersion, which can be visualized by placing a volume of dye tracer in an upstream location and watching how the dye disperses longitudinally as it moves downstream, takes into account the water flowing into and out of the streambed and adjacent bank sediments (hyporheic flow, see Section 3.2).

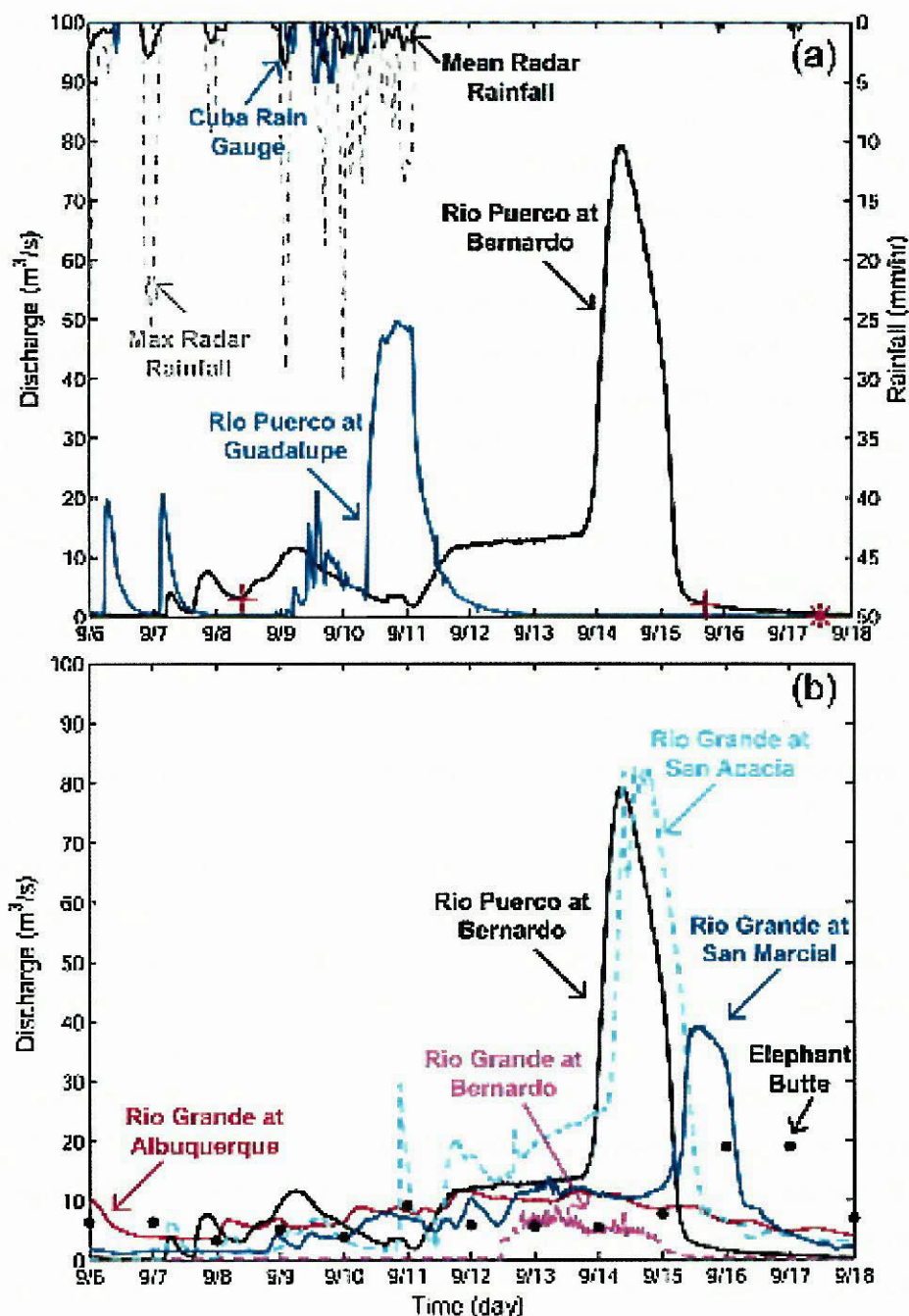


Figure 4-2. Time series of rainfall and streamflow observations in the Rio Puerco and Rio Grande, 6–18 September 2003.

Reprinted with permission from Vivoni et al. (2006).

Geomorphologic dispersion is the effect of different travel distances over the larger spatial scale of entire river networks (Rodríguez-Iturbe and Valdes, 1979; Gupta et al., 1980;

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1 Rinaldo et al., 1991; Snell and Sivapalan, 1994). Not all points along the river network (or even
2 headwater streams) are the same distance from the network outlet, so water entering the network
3 simultaneously will not arrive at the outlet simultaneously.

4 Considering only geomorphologic dispersion assumes water flowing through the
5 distribution routes moves at a constant velocity. Water velocity (and related hydrodynamics),
6 however, changes over space and time within river networks; for example, channel slope or
7 channel dimensions are not uniform across all pathways through the river network (Saco and
8 Kumar, 2002; Paik and Kumar, 2004). Kinematic dispersion is the effect of spatially variable
9 velocity of water as it moves through river networks (Saco and Kumar, 2002). The physical
10 configuration and the variable channel form of streams within a river network (which influence
11 components of hydrologic dispersion at varying scales) are the primary controls mediating the
12 arrival time of pulses in rivers following rain storms, dispersing the flow from streams to rivers
13 over time (Saco and Kumar, 2008).

14 Another factor that influences hydrologic response is transmission, or the loss of surface
15 flow volume due to infiltration into unconsolidated alluvium (see Section 3.2). Transmission is
16 another process in which streams, particularly in arid and semiarid regions, can slow or divert
17 water from downstream rivers and minimize downstream flooding. Over relatively short time
18 frames, transmission losses usually are dominated by infiltration or seepage through channel bed
19 and banks, but evapotranspiration losses can be significant in stream reaches with prolonged
20 surface flows (Hamilton et al., 2005; Costelloe et al., 2007). Because streams collect and
21 concentrate surface water, they tend to have more water available for infiltration, be more
22 permeable (have coarser sediment) than upland soils, have higher antecedent moisture, and be
23 closer to shallow groundwater, being the topographic low in catchments. Infiltration is
24 especially significant in arid, semiarid, and karst river networks, where water in intermittent and
25 ephemeral streams recharge groundwater aquifers (Brahana and Hollyday, 1988; Hughes and
26 Sami, 1992; Sharma and Murthy, 1995; Constantz et al., 2002). These aquifers supply water to
27 rivers and other water bodies downgradient.

28 Channel bed and bank permeability also governs the degree to which infiltration is an
29 important pathway between streams and groundwater aquifers. Fine bed and bank sediments
30 slow infiltration; in many semiarid and arid streams, bed sediments become finer in the
31 downstream direction because flow competence declines (Dunkerley, 1992). Because fine
32 sediments can become concentrated in channels following moderate flows, higher flows that
33 scour out fine sediments or submerge more permeable floodplains have higher infiltration rates
34 (Lange, 2005). In Walnut Gulch, Arizona, transmission losses over 54 km of channel resulted in
35 a 57% decrease in flow volume associated with a storm (Renard and Keppel, 1966). Tang et al.
36 (2001) used chemical and isotopic tracers to confirm that ephemeral streams are important areas

for floodwaters to recharge groundwater aquifers in desert regions, and infiltration losses accounted for up to half of the flow volume along three ephemeral channels in the southwestern United States (Constantz et al., 2002). Although transmission losses represent disruptions of surface connectivity between streams and downstream waters, such losses are hydrologic pathways that reduce downstream flooding and recharge groundwater aquifers that eventually support springs and flow in downgradient streams and rivers (Izbicki, 2007).

4.3.2. Sediment

Sediment carried with water flow from streams to downstream waters is critical for maintaining the river network. Fluvial sediments scour channels, deposit to form channel features, and influence channel hydrodynamics (Church, 2006). Although essential to river systems, excess sediment also can impair ecological integrity by filling interstitial spaces, reducing channel capacity, blocking sunlight transmission through the water column, and increasing contaminant and nutrient concentrations (Wood and Armitage, 1997).

Sediment in headwater streams originates from adjacent hillslopes and enters these streams via overland flow, bank erosion (Grimshaw and Lewin, 1980), and infrequent disturbances such as landslides and debris flows (e.g., Benda and Dunne, 1987; Swanson et al., 1998; Eaton et al., 2003). Sediment transported within river networks can be divided into two major categories: suspended and bed load. Suspended sediment is fine sediment (clay, silt, and fine sand) that requires slow velocities and little turbulence to remain entrained in the water column; bedload sediment is coarser particles that slide, roll, and bounce along the streambed during faster, more turbulent flows (Church, 2006; Wilcock et al., 2009).

The dynamic balance between sediment supply and transport capacity (Lane, 1955; Bull, 1991; Trimble, 2010)—with variables of sediment flux and sediment grain size on one side, and discharge and channel slope on the other side—is a principal paradigm of fluvial geomorphology. If one of these variables changes, a compensatory change occurs in at least one of the other variables. For example, if discharge increases, a lower channel slope is needed to transport the same amount of sediment of that grain size; alternatively, to move a load of fine sediment, less discharge or lower channel slope is needed relative to the same load of coarse sediment. Associated with this balance is the relationship between channel geometry (width and depth) and discharge (Leopold and Maddock, 1953), and adjustments to maintain a dynamic balance also can include channel dimensions. This balance is particularly relevant to geomorphologic connectivity in river networks because these variables commonly differ between streams and rivers (Ferguson et al., 2006; Ferguson and Hoey, 2008), with slope and grain size decreasing and discharge and channel size increasing downstream (Church, 2002). Thus, streams affect rivers through changing sediment supply or transport capacity at confluences.

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1 Relatively small contributions in sediment and discharge from a stream might elicit no detectable
2 change or only a short-lived spike in downstream sediment characteristics, discharge, or channel
3 geometry. In contrast, streams making large relative contributions at mainstem confluences elicit
4 strong stepped changes in mainstem characteristics. Because small streams can make large
5 contributions (e.g., floods, debris flows) during infrequent disturbances, even small streams have
6 long-lasting effects on rivers.

7 Streams transport and store sediment. Small streams tend to have low competence to
8 transport sediment during baseflow (Gooderham et al., 2007), but they have structures (boulders,
9 woody debris) that entrain and store colluvial sediments between infrequent disturbances (i.e.,
10 stormflows) that are the dominant means for downstream transport (e.g., Gomi and Sidle, 2003).

11 Ephemeral desert streams can exhibit high sediment export efficiency. The amount of
12 bed load per unit stream power from an ephemeral Negev Desert stream was estimated to be
13 substantially higher than from a forested perennial stream (Laronne and Reid, 1993). Despite
14 infrequent flows with short durations, flood waves (bores) in ephemeral desert streams carry
15 substantial amounts of sediment downstream (Hassan, 1990). The transport distance associated
16 with these floods, however, often is insufficient to link them to perennial rivers. For example, a
17 reach-scale study in Walnut Gulch, Arizona estimated sand transport distances of only 401 and
18 734 m in two consecutive years marked by nine floods (Powell et al., 2007). Streams also can
19 store substantial amounts of sediment that are only released during rare export events. A series
20 of experimental sediment introductions (to mimic road surface sediment) into steep, ephemeral
21 second-order streams in southwestern Washington revealed that between 30 and 45% of the
22 sediment (ranging from clay to coarse sand) was exported to the mainstem, 95–125 m
23 downstream, during stormflows representing 66–69% of bank full discharge (Duncan et al.,
24 1987). Virtually all of the fine clay particles introduced were exported from the ephemeral
25 streams to the mainstem, presumably because this fraction remained suspended at even moderate
26 flows (Duncan et al., 1987). Streams in the Coastal Range of Oregon stored 23% of the sediment
27 within a 2.5-km² basin compared with only 9% within the mainstem channel (May and
28 Gresswell, 2003). A long-term sediment budget for the Coon Creek watershed (360 km²), a
29 stream to the Mississippi River in Wisconsin, was constructed over periods coinciding with
30 major land use changes (Trimble, 1999). Over a period when agricultural practices caused major
31 soil erosion (1853–1938), streams acted as net sources of sediment (42×10^3 Mg y⁻¹); after
32 erosion control, streambank stabilization, and revegetation (1975–1993), streams changed to net
33 sinks of sediment (9×10^3 Mg y⁻¹; Trimble, 1999).

34 Several studies identify abrupt changes in sediment size and channel morphology
35 coinciding with stream confluences with sufficiently high symmetry ratios (Knighton, 1980;
36 Rhoads, 1987; Rice and Church, 1998; Rice et al., 2001). In his review of available data, Rhoads

(1987) determined that for a stream to create a discernible sediment or channel morphology discontinuity along a mainstem river, the symmetry ratio needed to be at least 0.7. A similar review of 168 confluences across the western United States and Canada found that a symmetry ratio needs to be greater than 0.2 to affect a downstream river's sediment supply or transport capacity (Benda, 2008). Suspended particulate matter (inorganic + organic) and bed particle size were measured above and below eight confluences on the Acheron River in Australia to determine stream contributions (Wallis et al., 2008; Wallis et al., 2009). Suspended particulate matter downstream of confluences approximated the sum of mainstem and stream exports during high flow, but stream contributions were negligible during low flows (Wallis et al., 2009). Four of the eight confluences showed expected changes in bed particle size below confluences with streams, and the bed particle sizes were similar in the mainstem and stream for the remaining confluences so particle size change associated with streams was not discernible (Wallis et al., 2008).

Streams, through their connections to rivers at confluences, can disrupt longitudinal trends in discharge of water and sediment in rivers (Best, 1988; Benda et al., 2004; Ribeiro et al., 2012). For example, dams often remove much of the sediment from transport, whereas most streams are sediment sources. The objective of a study on the Agigawa River in Japan was to examine contrasting disruptions associated with a dam (sediment removal) and a stream confluence (sediment discharge) located downstream from the dam (Katano et al., 2009). The stream contributions to the river reversed many of the dam-related changes to the river, including restoring the turbidity level and the proportion of sand and gravel substrate in the river bed (Katano et al., 2009).

4.3.3. Wood

Large woody debris (typically considered >10 cm diameter and >1 m long) has a strong influence on hydrodynamics, sediment transport and storage, and channel morphology (e.g., Harmon et al., 1986; Nakamura and Swanson, 1993; Abbe and Montgomery, 1996; Naiman and Decamps, 1997; Montgomery et al., 2003). More specifically, woody debris dissipates energy, traps moving material, and forms habitat for aquatic plants and animals (Anderson and Sedell, 1979; Harmon et al., 1986; Abbe and Montgomery, 1996; Naiman and Decamps, 1997; Gurnell et al., 2002). The debris can redirect water movements, create pools, and slow water movement through a channel (Nakamura and Swanson, 1993; Abbe and Montgomery, 1996; Naiman and Decamps, 1997). Wood recruitment to forested streams occurs as a result of chronic tree mortality; episodic disturbances such as fire, debris flows, landslides, and windthrow; and bank erosion. The steeper topography associated with hillslopes along many headwater streams

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1 increases the likelihood that trees will fall toward the channel (Sobota et al., 2006), relative to
2 streams in flatter terrain.

3 Wood tends to accumulate in, rather than be exported from, most forested headwater
4 streams, due to their low discharge and relatively small channel widths (Keller and Swanson,
5 1979; Bilby and Ward, 1989; Gurnell, 2003). For example, wood in a headwater stream in North
6 Carolina was determined to have entered the channel more than 60 years earlier (Wallace et al.,
7 2001) and more than a century earlier in some Pacific Northwest streams (Swanson et al., 1976;
8 Keller et al., 1981). Because of the large occurrence of wood and small size of streams, wood
9 has a stronger influence on hydrologic and geomorphic processes in headwater streams than in
10 most larger rivers (Bilby and Bisson, 1998). Large, infrequent disturbance events are the
11 primary drivers for wood movement in headwater streams (Benda and Cundy, 1990; Benda et
12 al., 2005; Bigelow et al., 2007). Reeves et al. (2003) determined that 65% of the wood pieces
13 and 46% of the wood volume in a fourth-order stream in the Coastal Range in Oregon were
14 delivered downstream by debris flows from headwater streams rather than the riparian zone
15 adjacent to the fourth-order channel. Using data from 131 reservoirs in Japan, investigators
16 identified a curvilinear relationship between watershed area and large woody debris export (Seo
17 et al., 2008), meaning that wood export per unit area increased from small streams (6–20 km²),
18 peaked at intermediate-sized streams (20–100 km²), and decreased from large streams
19 (100–2,370 km²). The amount of wood in low-gradient streams in the Midwest was determined
20 to be supply-limited mainly because human alteration depletes large wood sources and altered
21 hydrology and channel structure enhances transport of small wood downstream (Johnson et al.,
22 2006). Topography and topology also govern wood delivery from headwaters. Downstream
23 segments draining steep, finely dendritic networks will receive a greater proportion of wood
24 from headwater streams than networks that are low gradient and weakly dissected (Benda and
25 Cundy, 1990; Reeves et al., 2003).

26 Several studies have assessed the distribution of wood associated with confluences.
27 Wood volumes were measured upstream and downstream of 13 confluences (symmetry ratios
28 ranged from 0.05 to 0.49) in the Cascade Range of western Washington (Kiffney et al., 2006).
29 Wood volumes tended to peak at or immediately downstream from stream confluences (Kiffney
30 et al., 2006), suggesting that streams are either important sources of wood to mainstems or alter
31 channel form to enhance wood storage at confluences. Elevated wood density, however, was not
32 associated with confluences of eight streams to the Acheron River in Australia (Wallis et al.,
33 2009). The authors concluded that the study streams did not have sufficient capacity for
34 transporting wood to the mainstem, because streams had similar slope to the mainstem but lower
35 discharges (Wallis et al., 2009).

Large wood can shorten sediment transport and debris flow runout by entrainment (Lancaster et al., 2003). Woody debris in 13 Coastal Range streams in Oregon had accumulation rates ranging from 0.003 to 0.03 m³ m⁻¹ yr⁻¹, which were subsequently driven by time since the last debris flow (May and Gresswell, 2003). The volume of instream wood was strongly related to the volume of sediment stored. On average, 73% of stream sediment, prone to debris flow transport, was stored behind instream wood (May and Gresswell, 2003). Wood (and associated sediment) movement from headwater streams to downstream segments occurs through infrequent, high-magnitude events (e.g., debris flows, fire). Once in larger streams, wood and sediment can be stored in alluvial fans and floodplains between stormflows that trigger further downstream movement through the network (Benda et al., 2005). Because of the long distances and infrequent triggers associated with wood transport from most headwater streams to rivers, the relevant periods for governing transport are decades to centuries (Benda et al., 1998). Wood entering headwater streams can affect the downstream transport of water and materials in headwater streams, but also can be transported downstream from headwater streams where it is important habitat for aquatic life, a source of dissolved and particulate organic matter (POM), and influential in controlling hydrodynamics and channel morphology of rivers.

4.3.4. Temperature (Heat Energy)

Connections between streams and downstream rivers can affect water temperature in river networks (Knispel and Castella, 2003; Rice et al., 2008). Water temperature is an important physical factor governing the distribution and growth of aquatic life, both directly (through its effects on organisms) and indirectly (through its effects on other physicochemical properties, such as dissolved oxygen and suspended sediments; Allan, 1995). The primary factors governing water temperature in streams and rivers are climate (e.g., solar radiation, air temperature), water source (e.g., groundwater, runoff, meltwater), channel characteristics (e.g., width, bed topography, hydraulic exchange), topography (e.g., aspect, upland shading, canopy cover), and discharge (e.g., volume of water, turbulence; Poole and Berman, 2001; Caissie, 2006).

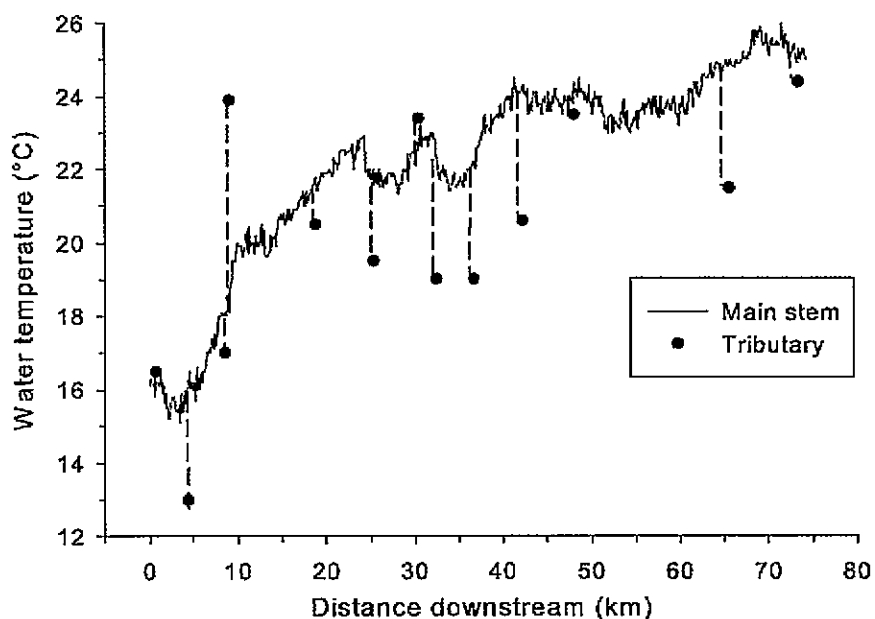
Perennial and intermittent streams that derive much of their flow from intermediate or regional groundwater have water temperatures similar to groundwater. Groundwater temperature is largely buffered from seasonal and short-term changes that affect air temperature, so that in temperate climates, groundwater tends to be cooler than air temperature in summer but warmer in winter. Streams deriving water from other sources (e.g., local groundwater, runoff, or snowmelt) have water temperatures and associated fluctuations reflecting these sources. Typically a nonlinear increase in mean daily water temperature occurs from headwaters to large rivers, and a unimodal trend is observed in daily variation (i.e., daily maximum-minimum) of

1 water temperature (Caissie, 2006). Stable groundwater temperatures (in headwater streams) and
2 greater depth and volume of water (in large rivers) buffer water temperatures from the daily
3 changes typical in intermediate-sized streams. The steep increase in water temperature
4 immediately downstream of headwaters is associated with more rapid flux of heat into small
5 streams, as shallow water contacts the surrounding air and receives direct radiation (Caissie,
6 2006). This longitudinal pattern, however, does not hold for all river networks, because some
7 river networks receive substantial deep groundwater contributions at lower reaches. As water
8 moves from streams through stream networks, water temperature is influenced by heat exchange
9 associated with solar radiation and hyporheic exchange (mixing with groundwater). These
10 factors vary with geographic location. For instance, water in headwater streams draining steep,
11 forested regions will be buffered from solar radiation and move downstream rapidly, compared
12 to a headwater stream draining a low-gradient, prairie catchment where shading by riparian trees
13 is minimal (see Section 4.7.2).

14 The empirical evidence supporting thermal connections between small streams and rivers
15 includes studies that have gauged the spatial relationship of water temperature over stream
16 networks and studies that have detected discontinuities in river temperature associated with
17 stream confluences. Geospatial analyses are used to assess the degree of spatial dependence of a
18 variable across a river network, and are particularly well suited for studying connectivity within
19 these systems. Water temperature data collected at 72 locations throughout a Catskill Mountain,
20 NY drainage basin were used to spatially predict daily mean summer water temperatures
21 throughout approximately 160 km of channel (Gardner and Sullivan, 2004). Results showed that
22 water temperatures at points along the river network separated by up to nearly 20 km were
23 related. Johnson et al. (2010) similarly used geostatistical analyses to determine the influence of
24 headwater streams on downstream physicochemistry, including water temperature. Water
25 temperature within the eastern Kentucky catchment was correlated across the river network over
26 an average distance of approximately 5 km (Johnson et al., 2010). Ebersole et al. (2003)
27 identified and characterized cold patches along a river network in northeastern Oregon that
28 largely had summer water temperatures exceeding the tolerance of native salmonids. Floodplain
29 springbrook streams were among the cold patches identified and were determined to contribute
30 the coldest water to the river network (Ebersole et al., 2003).

31 Thermal infrared sensors are a recent remote sensing tool that can provide snapshots of
32 thermal heterogeneity along river corridors (Torgersen et al., 2001; Torgersen et al., 2008;
33 Cristea and Burges, 2009). Thermal maps and plots of longitudinal profiles overlaid by the
34 locations of streams show that confluences coincide with distinct peaks and troughs in river
35 temperature (see Figure 4-3). The effect of streams was discernible when temperature

1 differences of streams and the mainstem exceeded 1°C and streams had large symmetry ratios
2 (Cristea and Burges, 2009).



4
5
6 **Figure 4-3. Airborne thermal infrared remotely sensed water temperature in**
7 **the mainstem and at tributary confluences of the North Fork John Day**
8 **River, OR, on 4 August 1998. Line indicates main stem, black dots indicate**
9 **tributary confluences, and dashed vertical lines indicate location of tributary**
10 **confluences along the mainstem.**

11 Reprinted with permission from Torgersen et al. (2008).
12
13
14

15 In most cases, the effect of the stream on river water temperature was minor in relation to
16 longitudinal changes over the course of the river (Torgersen et al., 2001; Cristea and Burges,
17 2009). Despite having a relatively minor effect on temperature over the length of entire rivers,
18 however, streams provide constant cold-water habitats that are important for aquatic life (see
19 Section 4.5.2).

20 21 4.4. CHEMICAL CONNECTIONS

22 Chemical connections are linkages between headwater and other tributary streams to their
23 downstream waters based on the transport of chemical elements and compounds, such as
24 nutrients, dissolved and particulate organic matter, ions, and contaminants. Chemical
25 connectivity between streams and rivers involves the transformation, removal, and transport of

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1 these substances; in turn, these processes influence water quality, sediment deposition, nutrient
2 availability, and biotic functions in rivers.

3 Because water flow is the primary mechanism by which chemical substances are
4 transported downstream, chemical connectivity is closely related to hydrologic connectivity (see
5 Sections 3.2 and 4.3.1). The movement of water across and through landscapes and into stream
6 networks integrates potential sources and sinks of solutes throughout the watershed, making
7 solute concentrations an integration of upstream mixing processes and transport processes in the
8 stream channel. A simplified characterization has streams operating in two modes: a
9 high-discharge throughput mode in which solutes and particles entering the stream channel are
10 quickly transported downstream, and a low-discharge processing mode whereby solutes and
11 particles are processed or stored in proximity to where they entered the stream network (Meyer
12 and Likens, 1979).

13 Factors that affect hydrologic connectivity (including precipitation patterns and human
14 alterations) modify these upstream-downstream chemical linkages. For example, the spatial and
15 temporal variability of rainfall affects chemical connectivity between tributaries and rivers.
16 Many small tributaries receive pulse inputs of water, sediment, organic matter, and other
17 materials during rain events. Periodic flows in ephemeral or intermittent tributaries can have a
18 strong influence on biogeochemistry by connecting the channel and other landscape elements
19 (Valett et al., 2005); this episodic connection can be very important for transmitting a substantial
20 amount of material into downstream rivers (Nadeau and Rains, 2007b). Alteration of channel
21 characteristics (e.g., channel shape and depth) and organic matter input also will affect the ability
22 of streams to cycle materials.

24 4.4.1. Nutrients

25 Alexander et al. (2007) investigated how nitrogen transport in a northeastern U.S. stream
26 network was affected by stream size, which ranged from headwater streams to large rivers.
27 First-order headwater streams contributed approximately 65% of the nitrogen mass in
28 second-order streams, and approximately 40% of that mass in fourth-order and higher order
29 streams (Alexander et al., 2007). Alexander et al. (2000) conducted a study of major regional
30 watersheds of the Mississippi River basin. Instream nitrogen loss was inversely related to mean
31 stream depth, most likely because denitrification and settling of particulate nitrogen occur less in
32 deeper channels, due to reduced contact and exchange between streamwater and benthic
33 sediments (Alexander et al., 2000). Both studies highlight how chemical connections are
34 affected by stream size, with small streams within the network affecting downstream water
35 quality.

1 Research in the Mississippi River basin on the hydrologic control and seasonality of
2 nutrient export from streams provides evidence of downstream connectivity from two studies
3 (see also Section 4.7.3). In the first, the export of dissolved reactive phosphorus from second-
4 and fourth-order streams in agricultural watersheds occurred mainly during conditions of high
5 discharge, with 90th percentile and greater discharges exporting 84% of the dissolved reactive
6 phosphorus primarily during January and June (Royer et al., 2006). Similar patterns have been
7 documented in total phosphorus concentrations of first- through fourth-order streams from
8 another Mississippi River basin watershed (Bayless et al., 2003). In the second study,
9 researchers focused on the January-to-June period to model riverine dissolved reactive
10 phosphorus yield of 73 watersheds as a function of nutrient sources and precipitation in the
11 Mississippi River basin. Jacobson et al. (2011) showed that riverine dissolved reactive
12 phosphorus yield was positively related to fertilizer phosphorus inputs, human sources of
13 phosphorus (e.g., sewage effluent), and precipitation. The surface runoff from precipitation
14 moves the phosphorus from fertilizer in fields into streams and rivers which transport them
15 downstream (Jacobson et al., 2011). These studies demonstrate the connections and processes by
16 which nutrients exported from streams in the Mississippi River basin contribute to anoxia in the
17 Gulf of Mexico (Rabalais et al., 2002).

18 The underlying geology of the Mokelumne River in the central Sierra Nevada of
19 California affected the spatial and temporal variability in chemical connections. Holloway et al.
20 (1998) examined water quality in that watershed to identify primary sources of nitrate entering
21 downstream reservoirs. They conducted a paired watershed comparison with two ephemeral
22 streams in adjacent catchments, which were underlain with different rock types (diorite vs.
23 biotite schist) but had similar land use, vegetation, topography, and catchment area. Many
24 samples from the diorite watershed had nitrate concentrations below detection limits (<4 µM),
25 with a median concentration of 3.3 µM; concentrations were not strongly associated with the
26 start or end of the high precipitation period. In the biotite schist watershed, maximum stream
27 concentrations of nitrate (>300 µM) occurred at the start of the high precipitation period, and
28 concentrations decreased over time. An adjacent perennial stream, also in a biotite schist
29 watershed, displayed this same temporal trend, with highest nitrate concentrations at the
30 beginning of the rainy season and decreasing concentrations during the spring. By monitoring
31 the stream network in this watershed, Holloway et al. (1998) concluded that biotite schist streams
32 in watersheds having this geological source of nitrogen, contributed a disproportionately large
33 amount of total nitrate to downstream reservoirs despite draining only a small area of the entire
34 watershed.

35 Chemical connectivity throughout a river network also is dynamic due to environmental
36 and biological processes. Nitrate concentrations were measured at 50 sites across the West Fork

1 watershed of the Gallatin River in the northern Rocky Mountains of southwestern Montana
2 under different hydrologic conditions and across two seasons, growing or dormant (Gardner and
3 McGlynn, 2009). Streams ranged from first-order mountain streams to fourth-order streams near
4 the West Fork-Gallatin River confluence. In the dormant season, the distance over which nitrate
5 concentrations were spatially correlated ranged from 3.2 to 5.5 km. In the growing season, this
6 range decreased to 1.9–2.7 km. This seasonal difference could have resulted from greater
7 biological uptake and use of nitrate during the growing season, limiting its transport by
8 streamflow; when these processes were reduced during the dormant season, greater spatial
9 dependence in nitrate concentrations was detected among sites.

10 Another example of seasonal variability in chemical connectivity was observed in the San
11 Pedro River in Arizona where differences in dissolved organic nitrogen concentration were
12 detected among three segments of the river during the dry season (Brooks and Lemon, 2007). In
13 the wet season, however, streamwater was well-mixed, the system was hydrologically connected,
14 and no differences in dissolved organic nitrogen concentration were detected (Brooks and
15 Lemon, 2007). The seasonal differences in the longitudinal pattern of nitrogen occurs because
16 nitrogen accumulates locally at varying levels during drier periods but is mixed and transported
17 downstream during large infrequent storm events, making nitrogen levels more longitudinally
18 uniform (Fisher et al., 2001).

19 Peterson et al. (2001) examined chemical connectivity by studying similar network
20 components across different types of stream networks. After measuring nitrogen export from
21 12 headwater tributaries distributed throughout the contiguous United States, Alaska, and Puerto
22 Rico, they found that uptake and transformation of inorganic nitrogen were most rapid in the
23 smallest streams (Peterson et al., 2001). Given the prevalence of headwater streams on the
24 landscape (see Section 4.2) and their hydrologic connectivity to other network components (see
25 Sections 3.2 and 4.3.1), this level of nitrogen processing could improve the water quality in the
26 downstream receiving waters. Other studies also highlight the processing of nitrogen in
27 headwater streams (e.g., Hill et al., 1998; Hill and Lymburner, 1998; Triska et al., 2007).
28 Mulholland et al. (2008) measured in situ rates of nitrate removal by denitrification and used
29 those rates to model how small and large tributaries in a network respond to simulated increases
30 in nitrate loading. At low loading rates, the biotic removal of dissolved nitrogen from water is
31 high and occurs primarily in small tributaries, reducing the loading to larger tributaries and rivers
32 downstream. At moderate loading rates, the ability of small tributaries to remove nitrogen is
33 reduced, but downstream the larger tributaries can remove the excess nitrogen. At high loading
34 rates, removal by small and large tributaries in the network is ineffective, resulting in high
35 nitrogen export to rivers (Mulholland et al., 2008). Similar results were obtained by Wollheim et
36 al. (2008) in the Ipswich River, MA.

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1 In the Ispwich River (MA) and Flat Creek (WY) networks, the effect of connectivity was
2 illustrated through simulation experiments by Helton et al. (2011) of a river-network model of
3 nitrate dynamics. The nitrate models under-predicted nitrogen removal in many reaches. That
4 under-prediction was attributed to connections between the river channels and adjacent wetlands,
5 which were thought to function as nitrogen sinks. The wetland functionality and connectivity
6 were not characterized by the model, resulting in the under-predictions (see Section 5.3.2.2).

7 The influences of headwater and other tributary streams on nutrient concentrations in
8 larger downstream waters, such as detailed in the examples given above, reflect the combined
9 processes of nutrient cycling and downstream transport that occur throughout the river network,
10 but most intensively in small tributaries. The concept of nutrient spiraling provides an approach
11 to quantifying these processes as well as a relatively simple framework for understanding their
12 implications. As nutrients cycle through various forms or ecosystem compartments, being
13 consumed and regenerated for reuse, they complete a “cycle” only after having been displaced
14 some distance downstream, thus in concept, stretching the cycle into a helix or “spiral” (Webster
15 and Patten, 1979). The stretching, or openness between loops, of the spiral is primarily
16 determined by flow, and the diameter of the loops is mainly determined by biotic activity
17 (Cummins et al., 2006). Nutrients such as dissolved phosphorus and nitrogen, which enter the
18 stream via groundwater or overland flow, are removed from the water column by streambed
19 algal and microbial populations. From there, the nutrients can be consumed by higher trophic
20 levels, detach and travel farther downstream as suspended particles, or return to the dissolved
21 pool through cell death and lysis. Nutrients flowing through the food web also are eventually
22 regenerated to the dissolved pool via excretion and microbial decomposition. In each phase of
23 the cycling process, the nutrient is subject to downstream transport, whether in dissolved,
24 particulate, or living tissue form, so that with each transition from one form to another it moves
25 some distance downstream. The average downstream distance associated with one complete
26 cycle—from a dissolved inorganic form in the water column, through microbial uptake,
27 subsequent transformations through the food web, and back to a dissolved available form—is
28 termed the “spiraling length.”

29 Measurement of total spiraling length requires detailed study of tracer dynamics through
30 multiple compartments of the stream ecosystem, but Newbold et al. (1981; 1983a) have shown
31 that it can be approximated by the “uptake length” or distance traveled in the water column
32 before microbial and algal assimilation occurs. Uptake lengths for phosphorus and nitrogen can
33 be estimated precisely only from tracer additions of radioactive or stable isotopes, but they can
34 be roughly estimated from experimental additions that briefly raise the concentration of the
35 natural form of the nutrient. Ensign and Doyle (2006) compiled results of 404 measurements of
36 uptake length of phosphate, ammonium, and nitrate in streams and rivers ranging from first to

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1 fifth order. For a given stream order, they estimated the number of cycles that each nutrient had
2 undergone as the ratio of median uptake length to the average length of stream for that stream
3 order (from Leopold et al., 1964). They found roughly that the three nutrient forms cycle
4 between 8 (nitrate) and 40 (ammonium) times within the length of a first-order stream, and
5 between 8 and 90 times within the respective lengths of first- to fourth-order streams.

6 Downstream ecosystems depend on ecosystem processes that occur in headwater streams.
7 Given that roughly half the water reaching larger tributaries and rivers originates from headwater
8 (first- and second-order) streams (see Section 4.3.1), the results of Ensign and Doyle (2006)
9 make clear that phosphorus and nitrogen arrive at downstream waters having already been cycled
10 many times in headwater and smaller tributaries. The cycling is, fundamentally, a complex of
11 ecosystem processes that intensively use nutrients and yet regenerate them to be delivered to
12 downstream waters much in their original form. Because nutrients undergo transformations
13 across various forms (e.g., dissolved, particulate, inorganic, living) while being transported
14 downstream (i.e., spiraling), explicitly identifying their exact origin to the network can be
15 difficult. If this cycling had been seriously impaired so that nutrient regeneration is inhibited, for
16 example, or nutrients in biologically unavailable or toxic forms are generated, then the
17 downstream effects could be large.

18 Although headwater nutrient cycling, or spiraling, functions largely to deliver regenerated
19 nutrients downstream, headwater processes measurably alter the delivery of nutrients to
20 downstream waters in many ways. Some of the nutrients taken up as readily available inorganic
21 forms are released back to the water as organic forms (Mulholland et al., 1988) that are less
22 available for biotic uptake (Seitzinger et al., 2002). Similarly, nutrients incorporated into
23 particulates are not entirely regenerated (Merriam et al., 2002; Hall et al., 2009), but accumulate
24 in longitudinally increasing particulate loads (Whiles and Dodds, 2002). The concentrations of
25 phosphorus and nitrogen that are delivered downstream by headwater streams have seasonal
26 cycles due to the accumulation of nutrients in temporarily growing streambed biomass
27 (Mulholland and Hill, 1997; Mulholland, 2004). Such variations have been demonstrated to
28 affect downstream productivity (Mulholland et al., 1995) and explain seasonality in spatial
29 correlations of nutrient concentration as described above. Nitrification, or the microbial
30 transformation of ammonium to nitrate, affects the form of downstream nutrient delivery.
31 Nitrification occurs naturally in undisturbed headwater streams (e.g., Bernhardt et al., 2002), but
32 increases sharply in response to ammonium inputs (e.g., Newbold et al., 1983b), thereby
33 reducing potential ammonium toxicity from pollutant inputs (Chapra, 1996). Denitrification,
34 which removes nitrate from streamwater through transformation to atmospheric nitrogen, is
35 widespread among headwater streams, as demonstrated by stable isotope tracer additions to 72
36 streams in the conterminous United States and Puerto Rico (Mulholland et al., 2008).

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Mulholland et al. (2008) estimated that small streams ($<100 \text{ L s}^{-1}$, about third order or less), free from agricultural or urban impacts, reduce downstream delivery of nitrogen by 20–40%. Alexander et al. (2007) and Wollheim et al. (2008), using earlier and less extensive measurements of denitrification rates, estimated nitrogen removal of 8 and 16% by headwater networks of orders 1–3 and order 1–5, respectively. In headwater agricultural streams, denitrification in stream sediments might not be effective at removing nitrate from streamwater because of altered hydrology. In these watersheds with tile drains and channelized headwaters, stream nitrate concentration is positively correlated with stream discharge, so these streams could be in a through-put mode whereby nitrate inputs to streams are rapidly transported downstream with little retention or processing (Royer et al., 2004).

Small tributaries also affect the downstream delivery of nutrients through abiotic processes. Meyer (1979) showed that phosphorus concentrations in a forested first-order New Hampshire stream were reduced by sorption to stream sediments. A much stronger sorption of phosphorus by stream sediments was observed by Simmons (2010) in first- to third-order West Virginia streams impacted by acid mine drainage. In the latter case, phosphorus sorbed to metal hydroxide precipitates introduced by mine drainage, illustrating the potential for headwater streams to absorb impacts while transforming them to downstream benefit.

4.4.2. Dissolved and Particulate Organic Matter

Headwater streams supply downstream ecosystems with organic carbon in both dissolved and particulate forms, which supports biological activity throughout the river network. Organic carbon enters headwater streams from the surrounding landscape, including wetlands (see Sections 5.3.2.4 and 5.4.3.1), in the form of terrestrial leaf litter and other seasonal inputs (e.g., catkins), dissolved organic carbon (DOC) in subsurface and surface runoff, and fine particulate organic matter in surface runoff including eroded soil. Ågren et al. (2007) determined that small headwaters exported the largest amount of terrestrial dissolved organic carbon on a per unit basis in the Krycklan watershed in Sweden. Organic carbon is also produced within the stream by photosynthesis. These inputs were first documented and quantified by Fisher and Likens (1973) for a forested headwater stream in New Hampshire. Fisher and Likens (1973) followed the fate of these inputs, concluding that 34% of the inputs were mineralized through respiration by consumers and microbes within the reach; this was the “ecosystem efficiency” of the reach. The remaining 66% was exported downstream constituting, as Fisher and Likens observed, “... inputs to the next stream section where they are assimilated, or passed on (throughput) or both.” Vannote et al. (1980) recognized that the exported carbon was not simply the unutilized fraction but was also greatly modified in character. They proposed, as one of the basic tenets of their River Continuum Concept, that longitudinal variations in the structure of stream ecosystems

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1 reflect, in part, the cumulative effects of upstream organic matter processing. Here we focus on
2 a subset of the large body of literature on organic matter dynamics in streams and rivers, citing
3 basic evidence that headwaters modify and export organic carbon that significantly affects
4 downstream ecosystem processes throughout the river network.

5 Most organic matter inputs (66%) to a headwater stream in New Hampshire were
6 exported (Fisher and Likens, 1973), which is comparable to results from other studies. Webster
7 and Meyer (1997) compiled organic matter budgets from 13 North American first- and second-
8 order streams. The median ecosystem efficiency was 31%, implying a median export of 69% of
9 inputs. Much or most of the organic carbon exported from headwater streams has been altered
10 either physically or chemically by ecosystem processes within the headwater reaches. Leaf litter
11 contributes an average of 50% of the organic matter inputs to forested headwater streams
12 (Benfield, 1997), but leaves and leaf fragments (>1 mm) only account for 2% or less of organic
13 matter exports (Naiman and Sedell, 1979; Wallace et al., 1982; Minshall et al., 1983). The
14 conversion of whole leaves to fine particles (<1 mm) involves physical abrasion, microbial
15 decomposition, and invertebrate feeding and egestion (Kaushik and Hynes, 1971; Cummins et
16 al., 1973; Petersen and Cummins, 1974). The rate of that conversion is affected by whether the
17 leaves are in an aerobic environment, such as riffles, or an anaerobic environment, such as
18 depositional pools (Cummins et al., 1980). Aquatic invertebrates that feed on leaves that have
19 entered streams are called shredders (Cummins and Klug, 1979; Cummins et al., 1989).
20 Invertebrate activity is particularly important, as demonstrated by large reductions of fine
21 particle export that followed experimental removal of invertebrates from a headwater stream
22 (Cuffney et al., 1990; Wallace et al., 1991). Strong invertebrate influence on fine particle export
23 also has been inferred from analysis of seasonal (Webster, 1983) and daily (Richardson et al.,
24 2009) variations. Headwater reaches also export organic carbon produced within the stream by
25 photosynthesis, both as dissolved organic carbon (Kaplan and Bott, 1982) and suspended
26 particles (Marker and Gunn, 1977; Lamberti and Resh, 1987).

27 Organic carbon exported from headwater streams is consumed by downstream
28 organisms, supporting metabolism throughout the river network. In part this results from direct
29 feeding by consumers on detrital organic matter (Wallace et al., 1997; Hall et al., 2000), but
30 much of the metabolic consumption of organic matter in streams occurs via microbial
31 decomposition (Fisher and Likens, 1973). The microbes themselves are then fed upon by
32 consumers (Hall and Meyer, 1998; Augspurger et al., 2008), whose energy in turn supports the
33 food web through what is known as the “microbial loop” (Meyer, 1994).

34 The organic carbon turnover length, derived from the spiraling concept (Newbold et al.,
35 1982a; see Section 4.4.1), is a measure of the downstream fate of exported carbon. Carbon
36 turnover length is computed as the ratio of the downstream flux of organic carbon to ecosystem

1 respiration per length of stream. It approximates the average distance that organic carbon is
2 expected to travel before being consumed and mineralized by aquatic biota. Carbon turnover
3 length for first-order streams is on the order of 1–10 km (Newbold et al., 1982a; Minshall et al.,
4 1983), suggesting that organic carbon exported from small streams is likely to be used primarily
5 in the somewhat larger streams of which they are direct tributaries (i.e., second- or third-order
6 streams). The carbon turnover length, however, actually represents a weighted average of widely
7 varying turnover lengths associated with the diverse array of particulate and dissolved forms of
8 organic carbon in stream and river ecosystems (Newbold, 1992). Turnover lengths of specific
9 forms can be estimated if their rates of downstream transport and mineralization (or assimilation)
10 are known. For example, Webster et al. (1999) estimated a turnover length of 108 m for whole
11 leaves in a North Carolina second-order stream whereas the estimate for fine (<1 mm) organic
12 particles was far longer at 40 km. Newbold et al. (2005) obtained similar estimates of 38 and
13 59 km for the turnover lengths of two different size fractions of fine organic particles in a
14 second-order Idaho stream. Similarly, Kaplan et al. (2008) concluded that dissolved organic
15 carbon in a third-order stream in southeastern Pennsylvania consisted of a rapidly assimilated
16 “labile” fraction with a turnover length of 240 m, a more slowly assimilated “semilabile” fraction
17 with a turnover length of 4,500 m, and a “refractory” fraction with immeasurably slow
18 assimilation, implying an indefinitely long turnover length sufficient, at least, to carry the carbon
19 to coastal waters.

20 Organic carbon that travels to a larger-order stream is likely to travel farther than its
21 original turnover length predicts, because turnover length increases with stream size (Minshall et
22 al., 1983; Webster and Meyer, 1997). For example, the organic turnover length of the Salmon
23 River, ID increased from 3.7 km in a second-order headwater to 1,200 km in the eighth-order
24 reach, about 600 km downstream from the headwaters (Minshall et al., 1992). In a modeling
25 study, Webster (2007) estimated that turnover length increased from several hundred meters in
26 the headwaters to greater than 100 km in a large downstream river. This progression of
27 increasing turnover length through the river continuum implies that organic carbon exported
28 from headwaters supports metabolism throughout the river network.

29 Although turnover length reflects the spatial scale over which upstream exports of
30 organic carbon are likely to support downstream metabolism, it does not provide direct evidence
31 for or quantify the actual use of organic carbon in the downstream reaches. Such evidence,
32 however, is provided by studies of transport and mass balance throughout the river network.
33 Shih et al. (2010) applied the SPARROW model to organic carbon (C) data from
34 1,125 monitoring sites throughout the conterminous United States. They estimated that all river
35 reaches (large and small) delivered an annual average of 72 kg C ha⁻¹ of incremental drainage
36 area, whereas the river systems as a whole exported 30 kg C ha⁻¹. Thus, 58% of the carbon

1 inputs were respired within the river networks, while the rest (42%) were transported
2 downstream. Shih et al. (2010) did not specify the proportion of inputs originating from
3 headwater streams but using their results with some assumptions, we can get a rough estimate
4 that river networks receive approximately a third of their organic carbon from headwater
5 streams. We begin with the proportion of carbon originating from allochthonous sources being
6 0.78 (Shih et al., 2010). If we assume that the proportion of headwater streams in a drainage area
7 is 0.50 (see Section 4.2; Alexander et al., 2007; Caruso and Haynes, 2011). Headwater streams
8 then provide $0.39 (= 0.78 \times 0.50)$ of the total organic carbon supply, with the input from the
9 larger downstream network being 0.61 (i.e., 61%) of the carbon supply. Using the ecosystem
10 efficiency for headwater streams of 31% (Webster and Meyer, 1997), we calculate that the
11 proportion of carbon originating in headwater stream that is delivered downstream is
12 $0.39 \times (1 - 0.31) = 0.27$. The proportion of carbon exported from headwater streams (0.27), plus
13 the proportion of carbon input directly to the downstream network (0.61), equals the carbon input
14 to the downstream network of 0.88. Thus, $0.31 (= 0.27/0.88 = 31\%)$ of the total carbon supplied
15 to downstream reaches originates from headwater streams.

16 Most terrestrial organic matter that enters headwater tributaries is transported
17 downstream (Gomi et al., 2002; MacDonald and Coe, 2007), typically as fine particulate or
18 dissolved organic matter (Bilby and Likens, 1980; Naiman, 1982; Wallace et al., 1995; Kiffney
19 et al., 2000). These small streams also can export significant amounts of autochthonous organic
20 matter via the downstream transport of benthic algae (Swanson and Bachmann, 1976). Both
21 allochthonous and autochthonous organic matter can be transported significant distances
22 downstream (Webster et al., 1999), especially during high flows (Bormann and Likens, 1979;
23 Naiman, 1982; Wallace et al., 1995). For example, Wallace et al. (1995) examined coarse
24 particulate organic matter export in three headwater streams in North Carolina and found that
25 63–77% of export over a 9-year period occurred during the 20 largest floods. This finding
26 suggests that headwater tributaries (including ephemeral and intermittent streams) can provide
27 temporary storage for organic matter (Gomi et al., 2002), which is then transported downstream
28 during storms or snowmelt. Exports also can vary seasonally, increasing in autumn and winter
29 when deciduous trees drop their leaves (Wipfli et al., 2007) and in the spring when flowers and
30 catkins are shed.

31 The amount of organic matter exported from headwater tributaries can be large, and often
32 depends on factors such as abiotic retention mechanisms within the channel (Bilby and Likens,
33 1980), biotic communities (Cuffney et al., 1990), and the quality and quantity of riparian
34 vegetation in headwater catchments (Wipfli and Musslewhite, 2004). For example, Wipfli and
35 Gregovich (2002) found that organic matter export ranged from <1 to 286 g of detritus (dead
36 organic matter) per stream per day in 52 small coastal streams in Alaska. When debris dams

1 were removed from a small stream in New Hampshire, export of fine particulate organic carbon
2 increased by 632% (Bilby and Likens, 1980); this finding illustrates the interdependence of
3 physical and biological connections within the river network.

4 Although organic matter clearly is exported from headwater tributaries, effects on
5 downstream biota, and how far these effects propagate down the river network, are difficult to
6 quantify (Wipfli et al., 2007). Many downstream biota rely on organic matter and its associated
7 microbes for food, but demonstrating where in the river network such material originates
8 presents a challenge. Similarly, the conversion of organic matter to other forms (e.g.,
9 invertebrate or fish biomass via consumption), having their own transport dynamics, makes
10 tracking sources of downstream contributions difficult. Given the prevalence of headwater
11 tributaries in both the landscape and the river network (Leopold et al., 1964), and their primacy
12 in organic matter collection and processing, concluding that they exert a strong influence on
13 downstream organic matter dynamics is logical. In addition, headwater tributaries also serve as a
14 source of colonists for downstream habitats. For example, headwater springs might provide
15 algae a winter refuge from freezing, then provide propagules that can recolonize downstream
16 reaches upon spring thaws (Huryn et al., 2005).

18 4.4.3. Ions

19 Measurements of ions and conductivity from nested study designs provide evidence for
20 connectivity by various transport mechanisms. Rose (2007) collected data at 52 sampling
21 stations in the Chattahoochee River basin, north-central Georgia, over a 2-year period. The basin
22 included the heavily urbanized Atlanta Metropolitan Region. The study sought to characterize
23 baseflow hydrochemistry across a rural-to-urban land use gradient. A plot of the major ion
24 concentrations (sodium, bicarbonate alkalinity, chloride, and sulfate) versus downstream river
25 distance showed distinct peaks relative to baseflow measurements in the Atlanta Metropolitan
26 Region, with elevated concentrations persisting downstream.

27 In a study of mined and unmined streams in the Buckhorn Creek basin in Kentucky,
28 water measurements taken at several locations within the same tributary had similar conductivity
29 values (Johnson et al., 2010). As expected, confluences disrupted this spatial similarity along the
30 river network. Conductivity values along the mainstem decreased at confluences with unmined
31 streams and increased at confluences with mined streams, demonstrating that streams were
32 transporting ions downstream and affecting downstream conductivity. This spatial pattern in
33 conductivity was consistent between spring and summer surveys of the stream network.

34 In a study in Sweden, measurements of pH from the outlets of seven catchments were
35 related to their headwater pH measurements in those catchments (Temnerud et al., 2010). Under
36 low-flow conditions, as pH at outlets increased, so did median pH of the headwater streams.

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1 This study illustrates the connectivity between the headwater components of the stream network
2 and the outlets of the catchments.

4 **4.4.4. Contaminants**

5 The movement of contaminants, or substances that adversely affect organisms when
6 present at sufficient concentrations, provides another line of evidence for chemical connectivity
7 between tributaries and the river network. Existing information typically has been derived from
8 empirical experiments using tracer substances released into streams to monitor movement along
9 a longitudinal gradient. In the case of trace metals, studies also have examined data collected at
10 multiple sites throughout a specific watershed, relative to a point source or a complex mixture of
11 point-source inflows (e.g., active mining areas or wastewater treatment plant discharges). The
12 studies using metals as tracers provide a way to understand sediment transport in streams and
13 rivers and to determine how metals are dispersed spatially and temporally in the watershed
14 (Rowan et al., 1995).

15 Another example of chemical connections along the river network is how inputs of water
16 associated with natural gas (coalbed methane) extraction and hardrock mining can influence
17 trace element and dissolved solute concentrations in perennial rivers. Patz et al. (2006)
18 examined trace elements and other water quality parameters in ephemeral tributaries resulting
19 from coalbed methane extraction activities connected to the perennial Powder River, WY. Iron,
20 manganese, arsenic, and fluoride and dissolved oxygen, pH, and turbidity differed across sample
21 locations, demonstrating connectivity between wellhead discharge and ephemeral channels. The
22 contribution of ephemeral channels was detected in the Powder River, where pH was
23 consistently elevated downstream of the confluence with a high-pH tributary (Patz et al., 2006).

24 In a broader study, Wang et al. (2007) investigated spatial patterns in major cation and
25 anion concentrations related to coalbed methane development in the Powder River basin
26 (33,785 km²) in Wyoming and Montana, using retrospective USGS data (1946–2002). The
27 study indicated that coalbed methane development could have detrimental effects on the Powder
28 River, especially concerning sodium adsorption ratio (sodicity). Although the authors indicated
29 connectivity and adverse affects in stream quality with increased sodium and stream sodicity,
30 data also revealed inconsistent patterns associated with complex spatial variability within the
31 basin (due to the geographic distribution of the coalbed methane wells). In addition, the use of
32 annual medians rather than monthly medians from the entire data set likely smoothed seasonal
33 variation inherent in the data.

34 The spatial extent of metal transport was shown in a study of the upper Arkansas River in
35 Colorado, where the headwaters have been affected by past mining activities (Kimball et al.,
36 1995). Bed sediments sampled from the headwaters to approximately 250 km downstream

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1 showed an inverse relationship between sediment concentrations of cadmium, lead, and zinc and
2 downstream distance. That same spatial distribution pattern in metals in bed sediments from
3 headwaters to downstream was observed for the Clark Fork River in Montana, which has been
4 impacted by mining and smelting activities in its headwaters (Axtmann and Luoma, 1991).
5 Based on regression models, metal concentrations in bed sediments from river sites were
6 inversely related to distance downstream, and predictions from those models indicated that
7 sediments with metals originating from the mining and smelting areas in the headwaters were
8 reaching Lake Pend Oreille, more than 550 km downstream. Hornberger et al. (2009) used a
9 19-year data set on sediments from the Clark Fork River with sites spanning from the
10 headwaters to 190 km downstream and found that copper concentrations in bed sediments at
11 downstream sites were positively correlated with concentrations at upstream sites.

12 In two studies examining the downstream transport of heavy metals to perennial systems
13 via ephemeral and intermittent channels, both Lewis and Burraychak (1979) and Lampkin and
14 Sommerfeld (1986) explored the impacts of active and abandoned copper mines in Arizona. In
15 the first study, water chemistry in Pinto Creek was monitored biweekly for 2 years at four
16 stations, one above and three below a point discharge associated with the Pinto Valley Mine in
17 east-central Arizona (Lewis and Burraychak, 1979). Surveys of fish, aquatic macroinvertebrates,
18 and vegetation were conducted during the same period at 13 sampling stations along the total
19 stream length. Contaminants from the Pinto Valley Mine entered Pinto Creek via accidental
20 discharge of tailings pond wastes (Lewis, 1977). Monitoring revealed that mine wastes
21 comprised up to 90% of total flow in Pinto Creek, and that most chemical parameters increased
22 in concentration below the discharge point, then decreased progressively downstream. Increases
23 in sulfate, conductivity, and total hardness between above-mine and below-mine locations were
24 most apparent, although increases in heavy metals and suspended solids were considered most
25 detrimental to biota. Suspended solids settled in and buried intermittent channels, which
26 contained up to 50 cm of mine waste sediment; these sediments were present all the way to the
27 stream terminus. Increased heavy metal concentrations in the food chain and sediments also
28 were detected below the discharge point.

29 An additional example of intermittent streams contributing highly mineralized, acidic
30 waters to a perennial tributary occurs in a study that characterized acid mine drainage impacts on
31 water and sediment chemistry (particularly major cations, silica, sulfate, selected heavy metals,
32 and acidity) in Lynx Creek, a small intermittent stream in east-central Arizona (Lampkin and
33 Sommerfeld, 1986). Six stations, two above and four below an abandoned copper mine, were
34 monitored (water and sediment samples) monthly for 1 year. Specific conductance, pH, and
35 dissolved ion concentrations varied with proximity to the mining complex. Concentrations of
36 most constituents were higher near the mine and progressively decreased downstream toward the

1 terminus of Lynx Creek due to precipitation and dilution by tributary streams. All heavy metals
2 and sulfate had significantly higher levels at the immediate discharge location versus the
3 above-mine stations; sulfate concentrations downstream of mine-drainage inputs also
4 significantly differed from the rest of the creek. Sediments throughout the creek were high in
5 metals, suggesting downstream transport of contaminated sediments. Acid-mine drainage from
6 the mine had a major but mostly localized impact on Lynx Creek. Evidence of connectivity was
7 apparent, with noticeable increases in dissolved metals, major cations, and sulfate and a
8 three-unit depression in pH.

9 Studies of the distribution, transport, and storage of radionuclides (e.g., plutonium,
10 thorium, uranium) have provided convincing evidence for distant chemical connectivity in river
11 networks because the natural occurrence of radionuclides is extremely rare. The production, use,
12 and release of radionuclides, however, have been monitored for military and energy production
13 for more than 50 years. Like metals, radionuclides adsorb readily to fine sediment; therefore, the
14 fate and transport of radionuclides in sediment generally mirrors that of fine sediment. From
15 1942 to 1952, prior to the full understanding of the risks of radionuclides to human health and
16 the environment, plutonium dissolved in acid was discharged untreated into several intermittent
17 headwater streams that flow into the Rio Grande at the Los Alamos National Laboratory, NM
18 (Graf, 1994; Reneau et al., 2004). These intermittent headwaters drain into Los Alamos Canyon,
19 which has a 152 km² drainage area and joins the Rio Grande approximately 160 km upriver from
20 Albuquerque. Also during this time, nuclear weapons testing occurred west of the upper Rio
21 Grande near Socorro, NM (Trinity blast site) and in Nevada. The San Juan Mountains in the
22 northwestern portion of the upper Rio Grande basin (farther upstream from the site where Los
23 Alamos Canyon enters the Rio Grande) are the first mountain range greater than 300 m in
24 elevation east of these test locations. The mountains therefore have higher plutonium
25 concentrations than the latitudinal and global averages because of their geographic proximity to
26 the test sites. The mountain areas are steep with thin soils, so erosion and subsequent overland
27 movement of plutonium from the testing fallout readily transported it to headwater streams in the
28 upper Rio Grande basin. The distribution of plutonium within the Rio Grande illustrates how
29 headwater streams transport and store contaminated sediment that has entered the basin through
30 fallout and from direct discharge. Los Alamos Canyon, while only representing 0.4% of the
31 drainage area at its confluence with the Rio Grande, had a mean annual bedload contribution of
32 plutonium almost seven times that of the mainstem (Graf, 1994). Much of the bedload
33 contribution occurred sporadically during intense storms that were out of phase with flooding on
34 the upper Rio Grande. Total estimated contributions of plutonium between the two sources to
35 the Rio Grande are approximately 90% from fallout to the landscape and 10% from direct
36 effluent at Los Alamos National Laboratory (Graf, 1994). Based on plutonium budget

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calculations, only about 10% of the plutonium directly discharged into Los Alamos Canyon and less than 2% of the fallout over the upper Rio Grande basin have been exported to the Rio Grande. Much of the plutonium is adsorbed to sediment and soil that has either not yet been transported to the river network or is stored on floodplains or in tributary channels (Graf, 1994). Approximately 50% of the plutonium that entered the Rio Grande from 1948–1985 is stored in the river and its floodplain; the remaining amount is stored in a downriver reservoir.

4.5. BIOLOGICAL CONNECTIONS

Biological connections are linkages between headwater streams, including those with intermittent and ephemeral flow, and their downstream waters that are mediated by living organisms or organism parts. In this section, we examine biological connections in terms of the materials (invertebrates, fishes, and genes) that move along river networks, and their effects on downstream waters (for discussion of particulate organic matter dynamics, see Section 4.4.2).

Because biological connectivity often results from passive transport of organisms or organism parts with water flow, these connections often depend on hydrologic connectivity (see Section 4.3.1). Many living organisms, however, can also actively move with or against water flow; others disperse actively or passively over land by walking, flying, drifting, or “hitchhiking.” All of these organism-mediated connections form the basis of biological connectivity between headwater tributaries and downstream waters.

Biological connectivity between upstream and downstream reaches can affect downstream waters via multiple pathways or functions. For example, headwater tributaries provide food resources to downstream waters. As Progar and Moldenke (2002) state, “...headwater streams are the vertex for a network of trophic arteries flowing from the forest upland to the ocean.” For downstream organisms capable of significant upstream movement, headwater tributaries can increase both the amount and quality of habitat available to those organisms. Under adverse conditions, small streams provide refuge habitat, allowing organisms to persist and recolonize downstream areas once adverse conditions have abated (Meyer and Wallace, 2001; Meyer et al., 2004; Huryn et al., 2005).

4.5.1. Invertebrates

Headwater streams provide habitat for diverse and abundant stream invertebrates (Meyer et al., 2007) and serve as collection areas for terrestrial and riparian invertebrates that fall into them (Edwards and Huryn, 1995; Kawaguchi and Nakano, 2001). These aquatic and terrestrial invertebrates can be transported downstream with water flow and ultimately serve as food resources for downstream biota. Many fish feed on drifting insects (Nakano and Murakami,

2001; Wipfli and Gregovich, 2002), and these organisms can also settle out of the water column and become part of the local invertebrate assemblage in downstream waters. However, drift has been shown to significantly increase invertebrate mortality (Wilzbach and Cummins, 1989), suggesting that most drifting organisms are exported downstream in the suspended detrital load (see Section 4.3.2).

The downstream drift of stream invertebrates (Müller, 1982; Brittain and Eikeland, 1988) and the contribution of terrestrial and riparian invertebrates to overall drift (Edwards and Huryn, 1995; Kawaguchi and Nakano, 2001; Eberle and Stanford, 2010) have been well documented. For example, drift estimates in 52 small coastal streams in Alaska ranged from 5 to 6,000 individuals per stream per day (Wipfli and Gregovich, 2002). The amount of invertebrate drift often is closely related to stream discharge (e.g., Harvey et al., 2006) and diel invertebrate behavioral patterns that are independent of flow (Rader, 1997). To compensate for loss of individuals to downstream drift, invertebrate populations in headwater streams are maintained and replenished by a combination of high productivity and upstream dispersal (Hershey et al., 1993; Humphries and Ruxton, 2002).

As with organic matter, assessing the effect of headwater invertebrate production and export on downstream waters is difficult. Wipfli and Gregovich (2002) estimated that drifting insects and detritus (i.e., particulate organic matter; see Section 4.4.2) from fishless headwater tributaries in Alaska supported between 100 and 2,000 young-of-year salmonids per km in a large, salmon-bearing stream. This estimate of headwater importance in systems where juvenile salmonids move into headwater tributaries to feed and grow is likely conservative (see Section 4.5.2). Other studies have shown increased fish growth with increased invertebrate drift (Wilzbach et al., 1986; Nielsen, 1992; Rosenfeld and Raeburn, 2009), indicating that drift does provide a valuable food resource, especially when food is limiting (Boss and Richardson, 2002).

Small streams also serve as habitat for invertebrates. Many invertebrate species are well adapted to seasonal or episodic periods of drying (Feminella, 1996; Williams, 1996; Bogan and Lytle, 2007) or freezing temperatures (Danks, 2007) and can be found throughout a range of stream sizes (e.g., Hall et al., 2001b) and flow regimes (intermittent and perennial, e.g., Feminella, 1996). After disturbance, these habitats can provide colonists to downstream reaches; this phenomenon can be especially important in intermittent streams, where permanent upstream pools can serve as refuges during drying. For example, Fritz and Dodds (2002, 2004) examined invertebrate assemblages before and after drying in intermittent prairie streams and found that initial recovery of invertebrate richness, richness of invertebrate drift, and richness of aerially colonizing insects were negatively related to distance from upstream perennial water. Intermittent streams can also provide refuge from adverse biotic conditions. For example, Meyer

et al. (2004) found that native amphipods can persist in intermittent reaches but are replaced by nonnative amphipods in perennial reaches.

4.5.2. Fishes

Although some fish species maintain resident headwater populations, many species move into and out of headwater streams at some point in their life cycles (Ebersole et al., 2006; Meyer et al., 2007). Some fish species occur only in small streams, which contribute to regional aquatic biodiversity (e.g., Paller, 1994). However, as with invertebrates, certain fish species can be found throughout a range of stream sizes (Freeman et al., 2007) and flow durations (Schlosser, 1987; Labbe and Fausch, 2000), and the fish species found in headwater streams often are a subset of species found in downstream habitats (Horwitz, 1978). Use of headwater streams as habitat is especially obvious for the many diadromous species that migrate between small streams and marine environments during their life cycles (e.g., Pacific and Atlantic salmon, American eels, certain lamprey species), and the presence of these species within river networks provides robust evidence of biological connections between headwaters and larger rivers. Return migration of diadromous fishes provides a feedback loop in which marine-derived nutrients are transported upstream to headwaters, for subsequent processing and export (see Section 4.4.1). Even nonmigratory taxa, however, can travel substantial distances within the river networks (Gorman, 1986; Sheldon, 1988; Hitt and Angermeier, 2008).

Hydrologic connectivity must exist for the exchange of fish between upstream and downstream reaches. Fish assemblages tend to be more similar among connected streams, in that assemblages in reaches located more closely together tend to have more species in common than in distantly separated reaches (Matthews and Robinson, 1998; Hitt et al., 2003; Grenouillet et al., 2004). Measures of river network structure also can explain fish assemblage structure, with studies showing that metrics such as link magnitude (the sum of all first-order streams draining into a given stream segment) and confluence link (the number of confluences downstream of a given stream segment) are significant predictors (e.g., Osborne and Wiley, 1992; Smith and Kraft, 2005).

For certain taxa, headwater tributaries provide habitat for a specific part of their life cycle. Many salmonids spawn in small streams, including those with intermittent flow (Erman and Hawthorne, 1976; Schrank and Rahel, 2004; Ebersole et al., 2006; Wigington et al., 2006; Colvin et al., 2009); many nonsalmonids also move into these habitats to spawn (Meyer et al., 2007). After spawning, these fish sometimes return downstream for feeding and overwintering. For example, Bonneville cutthroat trout moved from less than 1 km to more than 80 km downstream postspawning, typically within 30 days (Schrank and Rahel, 2004).

1 Many salmonids also grow in headwater streams (Brown and Hartman, 1988; Curry et
2 al., 1997; Bramblett et al., 2002). In some cases, these headwaters (including intermittent
3 streams) can provide higher quality habitat for juvenile fish, as evidenced by increased growth,
4 size, and overwinter survival in these habitats (Ebersole et al., 2006; Wigington et al., 2006;
5 Ebersole et al., 2009), perhaps due to warmer temperatures and higher prey and lower predator
6 densities (Limm and Marchetti, 2009).

7 In prairie streams (see Section 4.7), the importance of hydrologic connectivity is
8 especially evident, as many fishes broadcast spawn, or release eggs into the water column, which
9 then develop as they are transported downstream (Cross and Moss, 1987; Fausch and Bestgen,
10 1997); adult fish then migrate upstream prior to egg release (Fausch and Bestgen, 1997). Thus,
11 these fishes require hydrologic connectivity for egg development and upstream migration of
12 adult fish, to maintain populations (Fausch and Bestgen, 1997).

13 When abiotic or biotic conditions farther downstream in the river network are adverse,
14 upstream reaches can provide refuge habitat for downstream fishes. Examples of adverse abiotic
15 conditions include temperature (Curry et al., 1997; Cairns et al., 2005) or flow (Pires et al., 1999;
16 Wigington et al., 2006) extremes, low dissolved oxygen concentrations (Bradford et al., 2001),
17 and high sediment levels (Scrivener et al., 1994). Examples of adverse biotic conditions include
18 the presence of predators, parasites, and competitors (Fraser et al., 1995; Cairns et al., 2005;
19 Woodford and McIntosh, 2010).

20 Because headwater tributaries often depend on groundwater inputs, temperatures in these
21 systems tend to be warmer in winter (when groundwater is warmer than ambient temperatures)
22 and colder in summer (when groundwater is colder than ambient temperatures), relative to
23 reaches farther downstream (see Section 4.3.4; Power et al., 1999). Thus, these headwaters can
24 provide organisms with both warmwater and coldwater refuges at different times of the year
25 (Curry et al., 1997; Baxter and Hauer, 2000; Labbe and Fausch, 2000; Bradford et al., 2001). In
26 some cases, loss of coolwater refuges can facilitate invasion by species more tolerant of
27 warmwater conditions (Karr et al., 1985).

28 Headwater tributaries also can provide refuge from flow extremes. Fish can move into
29 headwaters (including intermittent streams) to avoid high flows downstream (Wigington et al.,
30 2006); fish also can move downstream during peak flows (Sedell et al., 1990), demonstrating the
31 bidirectionality of biological connections within these systems. Low flows can cause adverse
32 conditions for biota, as well, and residual pools, often fed by hyporheic flow, can enable
33 organisms to survive dry periods within intermittent streams (Pires et al., 1999; May and Lee,
34 2004; Wigington et al., 2006).

35 Biotic conditions within the river network—the taxa found in the system—also can create
36 an adverse environment, as the presence of invasive species or other predators and competitors

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can negatively affect native taxa. In some cases, headwater tributaries can provide these taxa refuge from other species and allow populations to persist. For example, Fraser et al. (1995) found that prey fish moved downstream when piscivores (fish-eating fish) were excluded, but moved upstream into headwaters when they were present. The role of headwaters as refuges from adverse biotic conditions can be closely related to where along the connectivity-isolation continuum these habitats fall, with isolation allowing for persistence of native populations (Letcher et al., 2007). Physical barriers (which reduce connectivity and increase isolation) have been used to protect headwater systems from invasion (Middleton and Liittschwager, 1994; Freeman et al., 2007); similarly, most genetically pure cutthroat trout populations are confined to small, high-elevation streams that are naturally or anthropogenically isolated (Cook et al., 2010).

When adverse conditions have abated and these organisms move back down the river network, they can serve as colonists of downstream reaches (Meyer and Wallace, 2001). Hanfling and Weetman (2006) examined the genetic structure of river sculpin and found that upstream populations were emigration biased (i.e., predominant movements were out of these reaches), whereas downstream populations were immigration biased (i.e., predominant movements were into these reaches).

4.5.3. Genes

Genetic connectivity results from biotic dispersal and subsequent reproduction and gene flow, or the transfer of genetic material within and among spatially subdivided populations. Populations connected by gene flow have a larger breeding population size, making them less prone to inbreeding and more likely to retain genetic diversity or variation—a basic requirement for adaptation to environmental change (Lande and Shannon, 1996). Genetic connectivity exists at multiple spatial and temporal scales. It can extend beyond a single river catchment (Hughes et al., 2009; Anderson et al., 2010), and in diapausing organisms, can be a direct link between distant generations (dispersal through time; Bohonak and Jenkins, 2003).

Although physical barriers can protect headwater habitats and populations by isolating them from colonization and hybridization with invasive species (see Section 4.5.2), isolation also can have serious adverse effects on native species via reductions in genetic connectivity. For example, Hanfling and Weetman (2006) found that man-made weirs intensified natural patterns of limited headwater immigration, such that headwater (above-barrier) sculpin populations diverged genetically from downstream (below-barrier) populations and lost significant amounts of genetic diversity. This pattern of strong genetic divergence accompanied by loss of headwater genetic diversity above natural and man-made barriers has been documented in multiple fish species and regions (Yamamoto et al., 2004; Wofford et al., 2005; Deiner et al., 2007; Guy et al., 2008; Gomez-Uchida et al., 2009; Whiteley et al., 2010). Loss of headwater-river genetic

1 connectivity might be exerting selection pressure against migrant forms in fish with life cycles
2 requiring movement along the entire river corridor (Morita and Yamamoto, 2002). Ultimately,
3 tradeoffs exist between the risks associated with headwater-river genetic connectivity (e.g.,
4 hybridization with nonnative species and hatchery fish) and those associated with genetic
5 isolation (e.g., reduced reproductive fitness, increased risk of local extinction, deterioration of
6 overall genetic variation, and selection against migratory traits; Fausch et al., 2009).

7 In general, genetic connectivity decreases with increasing spatial distance (Wright, 1943).
8 Genetic connectivity in river networks is also strongly influenced by the hierarchical structure of
9 a river network (see Section 3.4.2), the direction of dispersal (upstream, downstream, or both),
10 dispersal modes and pathways used (e.g., swimming, flying), and species life history (Hudy et
11 al., 2010).

12 Computer simulation approaches examine the spatial and temporal processes of genetic
13 connectivity for realistic behaviors and life histories of species inhabiting complex, dynamic
14 landscapes and riverscapes (Epperson et al., 2010). For example, Morrissey and de Kerckhove
15 (2009) demonstrated that downstream-biased dispersal in dendritic river networks (which by
16 definition have more tributaries than mainstems) can promote higher levels of genetic diversity
17 than other geographical habitat structures. Under these conditions, low-dispersing headwater
18 stream populations can act as reservoirs of unique genetic alleles (units of genetic variation) that
19 occasionally flow into and mix with highly dispersing downstream populations. Although the
20 number of headwater streams (i.e., potentially unique genetic reservoirs) is important in
21 maintaining genetic diversity, networks with more complex hierarchical structures (see
22 Figure 4-4) are more efficient at maintaining genetic diversity than networks in which all
23 tributaries flow directly into the mainstem (Morrissey and de Kerckhove, 2009). In another
24 simulation, Chaput-Bardy et al. (2009) demonstrated that out-of-network gene flow (e.g.,
25 terrestrial dispersal by insects or amphibians) or very high levels of within-network gene flow
26 (e.g., fish that move and reproduce throughout the network) can counteract the effects of network
27 structure; thus, individual species behavior can profoundly affect observed genetic patterns.

28 Most empirical evidence for the role of headwaters in maintaining genetic connectivity
29 and diversity comes from studies of economically important fish species, but correlations of river
30 network structure or landscape alteration with genetic patterns have been reported for other
31 species. Consistent with the model of Morrissey and de Kerckhove (2009), Fer and Hroudova
32 (2008) found higher genetic diversity in downstream populations of yellow pond-lily (*Nuphar*
33 *lutea*), which disperses over long distances via water-mediated dispersal of detached rhizomes.
34 Frequent dispersal and high gene flow among headwater and downstream populations of the
35 giant Idaho salamander (*Dicamptodon aterrimus*; Mullen et al., 2010) are expected to contribute
36 to genetic diversity of upstream and downstream populations.

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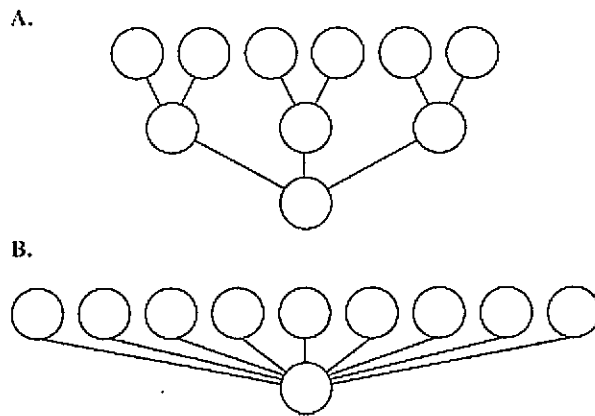


Figure 4-4. (A) A dendritic network with multilevel hierarchical structure, and (B) a uninodeal network with all headwater streams feeding directly into a river mainstem.

Modified from Morrissey and de Kerckhove (2009).

Headwater populations contribute to the maintenance of genetic diversity even in animals capable of overland dispersal. In a field study of the common stream mayfly *Ephemera invaria*, which emerges into streamside forests to mate and disperse, Alexander et al. (2011) found that regional genetic diversity is strongly correlated with tree cover in first-order (headwater) stream catchments. Observed loss of genetic diversity in this species could be related to degradation of stream habitats, degradation of out-of-network dispersal pathways, or both (Chaput-Bardy et al., 2009; Grant et al., 2010; Alexander et al., 2011).

In summary, genetic connectivity in river systems reflects the breeding potential of a metapopulation. The maintenance of genetic diversity is directly related to genetic connectivity, and thus is critical to a species' regional persistence. Genetic connectivity is influenced by the landscape, riverscape, and biology of the organisms involved; spatially subdivided stream and river populations can maintain genetic diversity, provided they remain connected by at least low levels of gene flow (Waples, 2010).